

CARNIVOROUS PLANT NEWSLETTER

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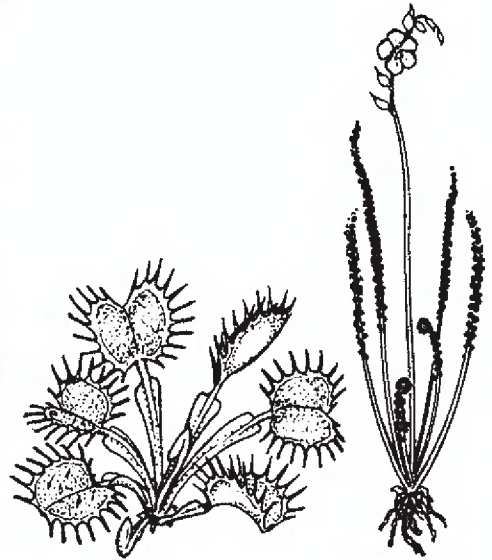




CARNIVOROUS PLANT NEWSLETTER

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Front Cover: The beautiful flowers of *Byblis rorida* (center left) and *Byblis pilbarana* (center right). Photo by Gregory Allan. Article on page 79.

Back Cover: *Byblis gigantea*. Grown indoor from seed by Anthony Bell. Article on page 89.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

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ICPS BOARD UPDATE

Over the new year, the ICPS Board went through a process of renewal. Our President, Marcel van den Broek, and Treasurer, Ryan Ward, both retired, and we welcomed three new Directors, John Brittnacher as Vice President, Cindy Slezak as Secretary and Membership Coordinator, and Daniela Ribbecke as Treasurer. As incoming President, I would like to pay tribute to, and thank both Marcel and Ryan for their contributions to the ICPS.

Marcel has served the society as a member of the Board of Directors since 2009, originally as Vice President and later as President. Over that time Marcel has overseen a number of significant achievements including: firmly establishing our presence on social media platforms such as Facebook, where we now have nearly 11,000 followers; our financial membership numbers have grown to over 1200 after seeing a decline during and immediately after the Global Financial Crisis; and changes to our Conservation agenda seeing funding for international projects, the IUCN-Carnivorous Plant Specialist Group and research projects.

During Ryan’s term on the Board he has taken on the difficult task of Treasurer and also moderated our Facebook forum. His enthusiasm and willingness to challenge and generate new ideas and solutions will be missed.

We are indeed fortunate that both Marcel and Ryan will remain connected to the ICPS as volunteers. Volunteers are the lifeblood of our society and we encourage anyone with the passion to get involved. One of our longstanding volunteers, Carolyn Becker, is stepping down from the important role of membership coordinator and we would like to convey our thanks and appreciation to Carolyn for her service.

The ICPS Board is delighted to have Daniela Ribbecke on the Board and John Brittnacher and Cindy Slezak back. Cindy and John have been driving forces within the ICPS since 2000, particularly in the day-to-day operations. Cindy’s business management experience helped make the ICPS into a functional corporation. John handled the websites and Seed Bank. Daniela brings considerable financial experience from her current role at California Carnivores.

With change comes the opportunity for renewal. I am pleased to announce that the Board overwhelmingly endorsed the creation of two new Director positions: Director Member Services and Director Marketing. Both of these positions are vacant. Anyone who would like to express interest is encouraged to send a CV and brief statement to our secretary, Keith Becker at keith@carnivorousplants.org.

Our mission statement remains unchanged and continues to guide what we do:

To provide for informational and educational exchanges on all aspects of carnivorous plants, to support horticultural and scientific studies of carnivorous plants, to encourage the cultivation, conservation, and appreciation of carnivorous plants, and to aid in the propagation and dissemination of carnivorous plants.

I am very interested to hear what our members are thinking and would encourage you to email your ideas and feedback to me at richardnunn@carnivorousplants.org.

—RICHARD NUNN, ICPS PRESIDENT

FIELD OBSERVATIONS OF *BYBLIS* IN AUSTRALIA

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Over the course of several field trips undertaken since 2014, I had the opportunity to encounter all currently described species of the genus *Byblis* (rainbow plants) in their natural habitats in northern and south-west Australia.

The eight species can be divided into two well-separated groups: Both species from south-west Western Australia (*B. gigantea* and *B. lamellata*) are perennial subshrubs and emerge from their fleshy roots (or from their above-ground stems) after the dry season or after a bushfire.

The second group is comprised by the six species from tropical northern Australia which are annual herbs and usually die off shortly after the wet season. If, however, the habitat remains even just barely moist, many species can grow and flourish well into the dry season which typically lacks any kind of precipitation. The next generation emerges from seeds after the start of the following wet season.

There is some controversy regarding the taxonomic status of several species and some researchers believe there may only be three or four morphologically clearly separated species in the genus *Byblis* (A. Cross, pers. comm.). In the following, I report on my personal observations and difficulties with distinguishing the species during my extensive travels through Australia.

Byblis aquatica (Fig. 1)

During my field trip to northern Australia in July 2014, I soon noticed that most locations where I knew *Byblis* should occur were already completely dried up. The dry season in this area usually lasts from May to October so July was right in the middle of it. However, after some searching, I came across a very sandy and slightly damp depression which can be flooded to a depth of around 50 cm during much of the wet season. This is a typical habitat of *Byblis aquatica* and I soon noticed some of the maroon-colored plants growing only about 5-10 cm in height with a 20-30 cm long, creeping stem.

A very characteristic feature of *B. aquatica* is the morphology of the stamens. It is one of only two *Byblis* species which produces anthers significantly shorter than their corresponding filaments (see Fig. 2). As in most other *Byblis* species, kleptoparasitic bugs of the genus *Setocoris* are very common on these plants. It is always amazing to observe how these little insects move along the sticky leaves with ease and feed on the captured prey!

Byblis aquatica is relatively common in the Darwin region of the Northern Territory and further east to Kakadu National Park with an additional distribution area known along the northern parts of Cape York peninsula, Queensland.



Figure 1: *Byblis aquatica* growing in a slightly moist habitat near Darwin during the dry season.

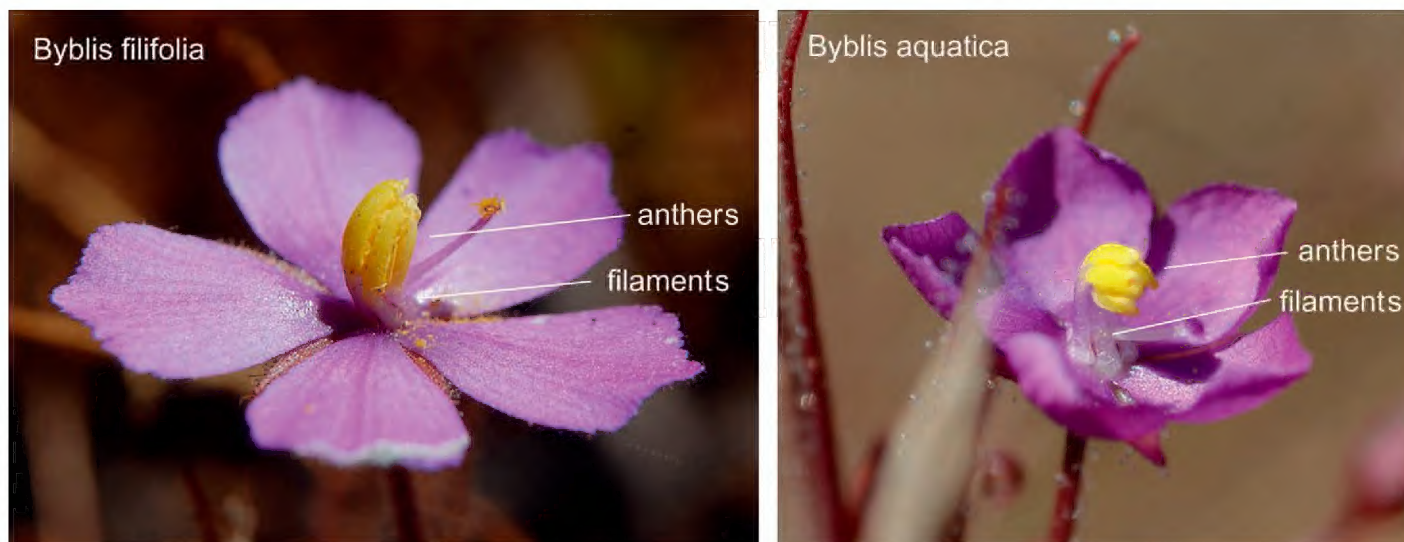


Figure 2: Comparison of the stamens of *Byblis filifolia* and *B. aquatica*.

Byblis liniflora (Fig. 3)

This is the only other species of the genus with very short anthers. During a dry-season visit to Litchfield National Park (which is ca. 80 km south of Darwin), I found this species growing in small crevices along the sandstone riverbed of a beautiful cascade. At most locations in the Northern Territory and the Kimberley region of Western Australia, *B. liniflora* seems to be a relatively small and inconspicuous plant typically occurring in very scattered populations of only a few individuals. However, at this cascade in Litchfield National Park, there were hundreds of spectacular and quite large plants growing on the bare sandstone rock. Some individuals measured more than 20 cm in diameter. I spent almost a full day exploring this location and discovered that there are no less than 15 additional carnivorous plant species growing within 50 meters of these *B. liniflora* – which means this is one of the most diverse sites I have ever visited in all my travels through Australia.

In March 2016 (i.e. during the wet season), I returned to the exact same cascade and instead of *B. liniflora*, the only thing I found was a raging river completely inundating the rock crevices where the plants grow during the dry season! It seems likely to me that, at least at this location, *B. liniflora* not only produces seed to survive the dry season, but to survive the raging floods of the wet season as well. The seeds seem to accumulate in the rock crevices and germinate as soon as the water level sufficiently recedes.

Byblis liniflora is closely related to *B. aquatica* and distinguishing these two can be challenging at times. The former species usually produces flower stalks which are significantly longer than in the latter, but that feature may not always be reliable. Furthermore, *B. aquatica* typically is a maroon colored plant while *B. liniflora* always produces a greenish



Figure 3: *Byblis liniflora* growing in Litchfield National Park.

color. Another possible way to distinguish them may be the length of the tentacles in relation to the leaf width. While the tentacles of *B. aquatica* are usually shorter than (or only slightly longer than) the width of the leaf, *B. liniflora* commonly produces tentacles more than two times as long as the leaf width. These features seem to be relatively stable when both species are cultivated under similar conditions (G. Allan, pers. comm.). Interestingly, I have never seen the two species co-occurring at the same location.

This is the *Byblis* species with the largest distribution area, ranging from the Kimberley region of Western Australia and the Top End of the Northern Territory to large parts of the Cape York peninsula and even Papua New Guinea. *Byblis liniflora* is the only species of the genus currently known to occur outside of Australia.

Byblis filifolia (Fig. 4)

Around 400 km to the south of Litchfield National Park lies the small town of Kununurra on the eastern edge of Western Australia's Kimberley region. In this area, the by far most common species is *B. filifolia* which grows in a wide range of seasonally wet habitats.

In contrast to *B. aquatica* and *B. liniflora*, the anthers of *B. filifolia* are longer than (or at least the same length as) their corresponding filaments (see Fig. 2). This species seems to be highly variable and some of the most interesting forms I encountered produce almost completely white flowers with the backsides beautifully striped in red and yellow.

Throughout most parts of the Kimberley, *B. filifolia* seems to be a very common species. Some additional populations are known in the Top End region of the Northern Territory.

Byblis rorida

This species has been the most elusive *Byblis* during my travels. Despite multiple attempts during both the dry and wet seasons, I was only able to find a single plant which fully matches Allen Lowrie's (2014) description of *B. rorida*.

Like in *B. filifolia*, the anthers of *B. rorida* are longer than or at least the same length as the filaments. However, it may be distinguished from *B. filifolia* by its sessile (stalkless) glands which cover the developing leaves and flower scapes. Another feature which can help with identification are the very long tentacles produced on the sepals. However, I often observed them in other species as well and the sessile glands also do not seem to be a reliable feature to distinguish *B. rorida* from its relatives. Therefore, it may be possible that this species just represents a particular form of the highly variable *B. filifolia* (A. Cross, pers. comm.).



Figure 4: Glistening *Byblis filifolia* near Kununurra, Western Australia.

Byblis rorida is endemic to the Kimberley region of Western Australia where it has mostly been found in the western parts.

Byblis guehoi (Fig. 5)

The approximately 200-km-long Dampier peninsula is located at the far western end of the Kimberley. During August 2014, I encountered a lot of *Byblis* plants growing throughout the peninsula in a variety of different habitats which included completely dry and recently burned *Eucalyptus* savannah, slightly damp wet-season flooded watersheds, and even permanently wet swamps. At most sites, the plants were growing together with *Drosera broomensis*, a member of the *D. petiolaris* complex.

All *Byblis* flowers seen had anthers longer than the filaments and since *B. filifolia* has never been recorded from this peninsula, I believed these plants to be either *B. rorida* or *B. guehoi*. The latter species is best known for its multi-branched growth habit, sometimes producing ten or more shoots. However, I soon realized that the species occurring across the peninsula are not easy to identify – even at the type location of *B. guehoi*! Most plants I found were not at all or only slightly branched and often produced very long tentacles on their sepals. Although these two characters would normally suggest *B. rorida*, sessile glands on the young leaves and flower stalks were constantly lacking. For this reason, it is likely that the plants I found there are exclusively *B. guehoi* (at least if considered to be a valid species, see below). This species is currently thought to be endemic to the Dampier peninsula.

Byblis guehoi was described based on particularly strongly branched specimens (A. Fleischmann, pers. comm.) and usually seems to be much less branched at most locations. At an extremely remote and permanently wet swamp located in the eastern part of the peninsula, I could finally find some highly branched specimens of *B. guehoi* which look relatively close to the type.

However, I could often observe multi-branching specimens in *B. filifolia* as well and, although currently thought to be geographically separated, these two species indeed seem to be very difficult or even impossible to distinguish.



Figure 5: Branched *Byblis guehoi* growing at a permanently wet swamp near the eastern coast of the Dampier peninsula.

Byblis pilbarana (Fig. 6)

The habitat of *B. pilbarana* – the most recently described species of the genus – is located more than 600 km to the southwest of the Dampier peninsula. Also called the Pilbara, this region differs markedly from the savannah landscape of northern Australia. With an average annual rainfall of only around 300 mm falling in one of the hottest places on earth (temperatures very close to 50°C are not uncommon during the summer months!), the Pilbara is characterised by a semi-arid desert

climate where carnivorous plants can only survive in very special niches.

One such a niche is “Red Rock”, an approximately 300 m wide and 40 m tall inselberg 60 km to the south of the mining town of Port Hedland. Due to its reddish color, “Red Rock” reminds me a little bit of the world-famous Uluru (Ayers Rock). Strangely, one of the worst aviation disasters of Australia occurred very close to this location on New Year’s Eve 1968, when a flight with 26 people on board crashed. A memorial and even some pieces of wreckage are located adjacent to the inselberg.

During my visit at the end of August 2014, I was only able to find ca. 20-30 individual specimens of *B. pilbarana* growing exclusively at the north-eastern edge of “Red Rock”. Interestingly, the only other carnivorous plant I could find in the whole Pilbara region (*Drosera finlaysoniana*), occurred only on the south-western, opposite end of the same rock where just six plants grew in a single crevice. These two spots are exactly the areas of the inselberg where the most water accumulates during rare rain events. Therefore, they remain moist for much longer than the surrounding areas. Snakes seem to prefer these slightly more humid places as well, because I encountered two of the most poisonous Australian snakes there: A brown snake (*Pseudonaja* sp.) in tall grasses and a young desert death adder (*Acanthopis pyrrhus*) on the bare rock.

Byblis pilbarana is a very impressive species with a relatively short and thick stem. It has anthers which are longer than the filaments and overall looks very similar to *B. filifolia* and *B. rorida*. It differs from the latter species by its unusual seeds and the absence of sessile glands on the developing leaves and flower stalks. However, the morphological differences between *B. pilbarana* and *B. filifolia*/*B. guehoi*/*B. rorida* seem to be quite minor and it is possible that all four may represent one highly variable species (A. Cross, pers. comm.).

This species is currently known from just a few locations around Port Hedland and it is the only carnivorous plant endemic to the semi-arid Pilbara region of Western Australia.



Figure 6: *Byblis pilbarana* growing at Red Rock.

Byblis lamellata (Fig. 7)

Even from the Pilbara, the distribution area of the two perennial *Byblis* species from south-west Western Australia is located more than 1,000 km to the south. During September 2014, I had the opportunity to thoroughly search the area around the small town of Eneabba which only has around 250 inhabitants. Eneabba is situated in the Mediterranean climate of the south-west which means September is actually part of the wet season! Accordingly, the predominant heathland vegetation of the area was full of beautiful flowers during that time. I was able to find many different *Stylidium*



Figure 7: An exceptionally large specimen of *Byblis lamellata* growing close to Eneabba.



Figure 8: *Byblis gigantea* growing in a swamp habitat near Perth.

species, the fascinating orchids of the genus *Caladenia* and of course lots of different tuberous and pygmy sundews growing between the flowering bushes. However, *B. lamellata* turned out to be an exceptionally difficult species to find!

Despite being described as “locally common” at several locations, it was only after a dedicated four-day long search when I first came across a single *B. lamellata*. But that plant was a beast! With a diameter of ca. 60 cm, the plant was about three to four times larger than anything I’ve seen in the tropical north and can be described as a true shrub due to its thick woody stem which develops more than 15 individual shoots. It was growing together with the pygmy sundew *Drosera eneabba* and the tuberous sundew *D. porrecta*.

On the same plant, I could again observe kleptoparasitic *Setocoris* bugs. But unlike the bugs from northern Australia, they were wingless and resembled ants due to their dark color. These bugs certainly belong to the species *Setocoris bybliphilus*.

Byblis lamellata seems to be a rare species only infrequently occurring at a few known locations around Eneabba and Warradarge, ca. 230 km north of Perth. Inadequate fire management and sand mining activities may be possible reasons for the apparent decline in population numbers (A. Cross, pers. comm.).

Byblis gigantea (Fig. 8)

This species has an even more southerly distribution area. It occurs in a narrow area around the large city of Perth where it is only known from four relatively small populations. Despite extensive searches, I was unfortunately not able to locate any additional sites. Furthermore, I could only find four individual plants of *B. gigantea* at the two known locations I visited. This species is certainly the rarest and most threatened of all *Byblis*!

Its habitat differs significantly from the dry, sandy habitat of *B. lamellata* since it only

occurs in seasonally wet swamps where moisture is present for a large part of the year. Therefore, other carnivorous plants which are favoring damp habitats (i.e. *Drosera occidentalis*, *D. myriantha*, *D. nitidula* and *Utricularia petertaylorii*) can be found growing together with *B. gigantea*.

Despite being geographically well separated and occurring in very different habitats, *B. gigantea* and *B. lamellata* are very closely related and distinguishing them based on morphological features is very difficult or even impossible. While *B. gigantea* typically only resprouts from its underground rootstock after the dry season or after a fire, *B. lamellata* often produces an aerial stem from which it can resprout. However, the two species produce quite different seeds, and this may be the most reliable morphological feature to distinguish them.

Reference

Lowrie, A. 2014. Carnivorous Plants of Australia: *Magnum Opus*, volumes 1, 2, 3. Redfern Natural History Productions Ltd., Poole.

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EVIDENCE OF MOTILE TRAPS IN *BYBLIS*

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Introduction

Byblis Salisb. is a small genus of carnivorous plants with adhesive traps in the Lamiales family Byblidaceae Domin. There are two perennial species (*B. gigantea* Lindl. and *B. lamellata* Conran & Lowrie) with restricted ranges in Western Australia, where they experience a Mediterranean climate. The critically endangered *B. gigantea* is endemic to the Swan River drainage area, now entirely within the Perth metropolitan area, whilst *B. lamellata* is restricted to the coastal region North of Perth. The genus also contains six currently recognized annual species (*B. aquatica* Lowrie & Conran, *B. filifolia* Planch., *B. guehoi* Lowrie & Conran, *B. liniflora* Salisb., *B. pilbarana* Lowrie & Conran, and *B. rorida* Lowrie & Conran) which inhabit the tropical and semi-arid regions of Northern Australia. The genus also extends to the island of New Guinea (Lowrie 2013; McPherson 2010). All species are found in substrates which are very nutrient-poor (Lowrie 2013; McPherson 2010) and share habitats with representatives of other genera of carnivorous plants (particularly *Drosera*, but also *Utricularia* and *Nepenthes*). Although there are important morphological differences between the *Byblis* species, all share the same basic structure in that they produce stems from which radiate filiform leaves. Another feature common to all species is the ability to produce fast concentrated growth in response to seasonal rainfall. (Bourke, pers. comm.). It has been observed on many occasions that all *Byblis* species play host to Miridae bugs from the genus *Setocoris* (Bourke, pers. comm.). A mutualistic relationship has been proven to exist between another viscid plant genus *Roridula* and a different genus of the family Miridae, *Pameridea* (Anderson & Midgley 2003). A similar relationship is strongly suspected in *Byblis* (Lowrie 2013; Cross *et al.* 2018).

The basic structures which facilitate carnivory in *Byblis* are well-established. Virtually all above-ground parts of the plant, including the stems, pedicels, and sepals, are covered liberally in glands of two types. The first type is “stalked glands”, each of which is furnished with a droplet of secreted mucilage and is positioned atop a stalk (often referred to as a “tentacle”), which consists of a single elongated cell (Darwin 1875; Lloyd 1942) and can be up to 2.6 mm in length (McPherson 2010), although length varies across species and plant organ.

The glands of the second type are far smaller and are positioned in rows within grooves in the epidermis (Lloyd 1942). They are believed to be responsible for secretion of digestive fluids and absorption of digested matter (Cross *et al.* 2018). Although these glands are frequently referred to as “sessile glands”, this classification is erroneous, as each rests upon an even smaller stalk cell, so does not emerge directly from the epidermis (Lloyd 1942; McPherson 2010). Accordingly, they can more appropriately be called “digestive glands”.

These details notwithstanding, the carnivorous syndrome in *Byblis* has been under-studied relative to that of other carnivorous plants. Although it has long been recognized that the glands and cellular structure of *Byblis* appear to be clearly adapted to facilitate secretion and absorption of the kind associated with the capture of prey and sequestration of nutrients (Darwin 1875; Lloyd 1942), the carnivorous nature of the genus has been disputed. Bruce (1905) observed apparent digestion of albumen by *B. gigantea*, but Lloyd (1942) was unable to perceive evidence of digestion of carmine fibrin during a two-week period within which he had access to live specimens of the

same species. Moreover, Hartmeyer (1997) concluded that *B. liniflora* does not produce proteases on the basis that the plants (unlike specimens of various species (and one hybrid) of the genus *Drosera*) did not digest the gelatine layer of strips of photography film attached to the lamina, even when provided with stimulation 12 hours previously in the form of a 10% yeast solution. Accordingly, at least some species have on occasion been indicated as not “truly” carnivorous by some authors (see generally D’Amato 1998; Rice 2006).



Figure 1: Cultivated *Byblis liniflora* with cheese that is in the process of being digested.

In 2005, however, Hartmeyer (2005) used the aforementioned film-strip tests to provide evidence of protease production by *B. filifolia*, and Płachno *et al.* (2006) used enzyme labelled fluorescence to demonstrate phosphatase secretion by the digestive glands of *B. liniflora*. Additionally, the author of this article has obtained tentative evidence of protease production by *B. gigantea* and *B. lamellata* by using Hartmeyer’s film-strip tests, and casual observations on the basis of the experiments detailed below showed apparent evidence of digestion of animal proteins in all currently recognized species (see cheese on *B. liniflora* in Fig. 1). Most compellingly, however, Skates (2016) deployed stable isotope techniques on *B. gigantea*, *B. liniflora*, *B. filifolia*, and *B. rorida* to demonstrate conclusively that these species are able to sequester significant quantities of nitrogen from captured prey. Although more research is required regarding the precise composition of the digestive fluids of *Byblis*, and of the factors which provoke their secretion, it may be postulated that the failures to detect digestion may be attributable to the fact the secretions of the digestive glands, but not the stalked glands, contain digestive enzymes. Moreover, it may well be that certain types of chemical stimulation are necessary to provoke secretion of digestive enzymes.

The traps of *Byblis* have been classified as non-motile (“passive”) since the earliest investigation of their carnivorous properties, which was performed by Darwin using dried specimens of *B. gigantea* (Darwin 1875). Darwin posited that the unicellular nature of the stalks (called “pedicels” by Darwin) of *B. gigantea* rendered gland motility impossible because “no instance is known of unicellular structures having any power of movement” (Darwin 1875, p 344). He took the view that prey captured by the stalked glands would “...probably sink down besmeared with the secretion and rest on the small sessile glands” (Darwin 1875, p 344). Darwin’s classification of *Byblis* as passive carnivores has essentially been accepted ever since, both in scientific works (Lloyd 1942; Juniper *et al.* 1989; Lowrie 1998, 2013; Ellison & Adamec 2018) and popular texts (Slack 1979, 1986; D’Amato 1998; Rice 2006; McPherson 2008, 2010). It should be noted that Darwin undertook no experiments to investigate the process of carnivory in *Byblis*, and that he only studied dried plant material of a single perennial species, presumably for want of access to living plants.

There is some minor discord regarding the precise process of carnivory in *Byblis*. According to McPherson (2010, p 966), upon stimulation from captured prey, both the stalked and digestive glands produce “copious secretions [which cause] it to become affixed directly to the leaf blade and in contact with the digestive, enzyme-secreting sessile glands”. In this respect, the carnivory of *Byb-*

lis has often been thought similar to that of the monotypic genus *Drosophyllum*, a carnivorous plant which has some superficial morphological similarities to *Byblis* and which has been demonstrated to capture prey using secretions from immobile stalked glands, and to effect digestion and absorption via sessile glands (Cross *et al.* 2018). Notably, the carnivorous syndrome in *Drosophyllum* has been investigated far more thoroughly than that of *Byblis*. For the purposes of this article, it is particularly pertinent to note that Darwin (1875) conducted experiments on live plants which proved that its stalked glands are incapable of movement. A slight variant of the process in *Byblis* has been suggested whereby secretions from the stalked glands are primarily responsible for producing a “pool of fluid” in which “the prey is dissolved” (Lowrie 1998, p 16), and that the sessile glands are responsible solely for absorption of the products of digestion (Lowrie 1998; Bourke & Nunn 2012).

A rationale for the research in this paper

There are certain respects in which the orthodox account of passive carnivory in *Byblis* does not stand up to scrutiny. *Byblis* possess morphological characteristics which suggest that, despite Darwin’s insinuation to the contrary, gravity is unlikely in many instances to play a key role in the migration of captured prey from the stalked glands to the digestive glands. In *Byblis*, the stalked glands are most densely concentrated on the underside of the leaves, and observations of cultivated plants show that this is a frequent site of prey-capture (see also Slack 1979, p 96). Observations of specimens of *B. filifolia*, *B. liniflora*, and *B. rorida* at natural location indicate that the most common prey items are small flying insects which may be trapped and digested on any part of the leaf, including the underside (Bourke, pers. comm) (see Fig. 2). Moreover, at least in *B. filifolia* and *B. rorida*, captured and digested prey are often found adhered to the vertical stems, perhaps a consequence of doomed attempts to escape. (Bourke, pers. comm.) (see Fig. 3 left). It is also relevant to note that newly unfurled leaves are often more or less upright, whilst older leaves, especially in the annual species, usually radiate horizontally or semi-erectly from the stem. Consequently, prey is often captured in such a manner that any migration of that prey onto the leaf surface must be in an upward or horizontal direction (Fig. 3 right). Only towards the end of their active life do leaves radiate predominantly downwards so as to maximize exposure of the upper leaf surfaces and encourage prey to be captured in a position which allows for it to migrate towards the digestive glands in a downward direction, as described by Darwin.

The notion that copious secretions may be predominantly responsible for bringing prey into contact with the leaf surface and digestive glands thereon is also inconsistent with the morphology of most *Byblis* species. This can be seen when comparing *Byblis* with the superficially similar *Drosophyllum*. The latter genus has the glands and leaves arranged in a similar manner to those of *Byblis*, and the two genera have been described as exhibiting essentially the same

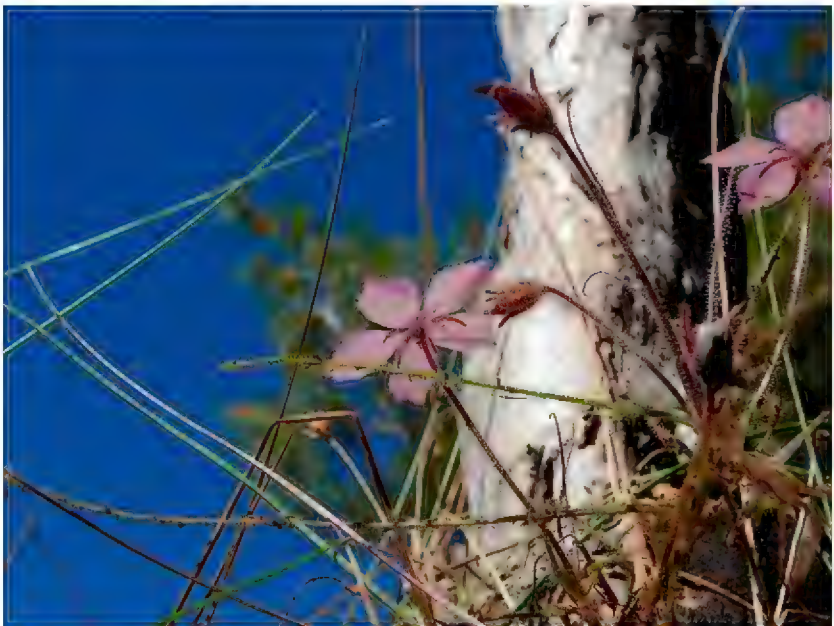


Figure 2: Prey adhered mainly to the underside of leaves of wild *Byblis filifolia* (photo by Andreas Fleischmann).



Figure 3: Wild *Byblis rorida* with prey adhered to stem (left, photo by Greg Bourke); wild *Byblis filifolia* with many lower leaf surfaces well-positioned to capture prey (right, photo by Andreas Fleischmann).

process of trapping and digestion (Darwin 1875; McPherson 2008, 2010; Slack 1979). In fact, the structure of the traps of the two genera is extremely different, and *Byblis* is not morphologically suited to utilizing the mode of carnivory that has been proven in *Drosophyllum*. Most crucially, *Drosophyllum* stalks, unlike those of *Byblis*, are multicellular and vascularized, and produce mucilage continuously (Lloyd 1942). The stalked glands of *Drosophyllum* are very short, so that captured prey is always within very close proximity to the leaf surface and the digestive glands. Thus, copious mucilage secretions from stalked glands provide a ready medium through which digestive fluids can travel the short distance from the leaf surface to the prey. This arrangement also produces ideal conditions for prey to be drawn into contact with the digestive glands by capillary action.

In contrast, *Byblis* stalks are not vascularized, and are thus unsuitable for continuous mucilage secretion. Also, the stalked glands of most *Byblis* species are comparatively long, and would require especially copious secretions in order provide a medium by which the prey could come into contact with the digestive secretions. Moreover, in thread-like leaves which are erect or semi-erect, gravity might cause secretions to run down the leaf before enveloping the prey sufficiently to provide a connection with the leaf surface, resulting in a potentially very inefficient trapping strategy. It is also notable that there is a distinct lack of published photos of *Byblis* plants showing prey adhering to the outer stalks that is enveloped by sufficiently copious mucilage secretions to form a connection with the leaf surface/digestive glands. This correlates with observations made in the private collection of the author.

The possibility of motile (“active”) traps in *Byblis* was first suggested publicly in 2009 by Cindy Chiang, an amateur horticulturalist who is very skilled at cultivating annual *Byblis* in her

native Singapore. Chiang posted a photograph on the ICPS internet forum of a freshly caught fly on a *B. guehoi* specimen, and another photograph taken a few hours later which, she thought, suggested that the fly had been drawn closer to the leaf surface. Moreover, causal observations made over many years in the author's private collection suggested that it is common for plants of all species of *Byblis* to be seen with dry prey stuck to the leaf surface, especially on the underside of the leaves, a position in which the prey is most unlikely to have settled without some intervention from the plant. This phenomenon can also be observed in some published photographs of *Byblis* species in habitat (e.g. McPherson 2008, p 255 and 267; McPherson 2010, p 955; Lowrie 2013, p 204).

Materials and methods

The experiments all involved placing small fragments of animal-derived protein matter (and sometimes, for comparison, inorganic matter) on the stalked glands of specimens of all *Byblis* species and observing the reaction of the stalks and glands. Although the fragments were predominantly placed on the stalked glands of the leaves, some were also placed on the stalked glands of pedicels and stems. Particular care was taken to ensure that the fragments were placed in a manner which ensured that they were not in contact with the surface of the leaf, pedicel, or stem. Accordingly, none of the fragments were initially in contact with digestive glands.

Over a period of three years, experiments were repeatedly conducted on cultivated specimens of *B. aquatica*, *B. filifolia*, *B. gigantea*, *B. guehoi*, *B. lamellata*, *B. liniflora*, *B. pilbarana*, and *B. rorida*. The selected *B. gigantea* and *B. lamellata* specimens were mostly greenhouse-cultivated, whilst the annual species were mostly specimens grown indoors in a heated terrarium under fluorescent lights. The experiments involved placing small fragments of flake fish food (consisting primarily of fish, mollusc, and crustacean meal), cheese, and dried bloodworms on the stalked glands of leaves, pedicels, and stems. The varied food fragments had a maximum diameter of approximately 3 mm. Except with *B. aquatica* (see below), the fragments were always placed on glands with long stalks so that they were the maximum possible distance from the digestive glands. Stalked glands on the underside of the leaves and (where relevant) pedicels were selected: depending on whether the leaf or pedicel in question was upright or horizontal, this was done in order to eliminate or mitigate any effects of gravity. In *B. aquatica*, the gland stalks are extremely short (usually well under 1 mm in length), so it was not possible to ensure that the fragments were any significant distance from the digestive glands. Also, a detached wing of a small fly, and a detached and dried abdomen of another small fly, were placed in a similar fashion on glands of an adult *B. liniflora* specimen. The fragments were observed at regular intervals over 24-48-hour periods. Although most experiments were conducted on healthy plants, some observations were also made of plants grown in sub-optimal conditions (such as *B. filifolia* plants on a windowsill in November in the United Kingdom with no artificial lighting).

To compare the reaction to animal proteins and other matter, an experiment was conducted whereby ten fragments each of perlite and kitchen paper (similar in size to the fragments mentioned above) were placed on stalked glands of four greenhouse-cultivated specimens of *B. gigantea* and one of *B. lamellata*. The fragments were observed at regular intervals over a 72-hour period. Two of the cheese fragments were placed on old leaves which, although still producing mucilage from the stalked glands, were beginning to turn brown at the leaf tips. Similar, albeit more casual, experiments with inorganic matter were also conducted on *B. filifolia*, *B. guehoi*, *B. liniflora*, *B. pilbarana*, and *B. rorida*.

As will be discussed below, the observations made as a result of the above experiments yielded some very surprising and interesting results. In order to scrutinize more carefully the reaction of the plants to the placement of the fragments, several time-lapse videos of stalk cell movement were produced using fragments of flake fish food, cheese, or dried bloodworms (see https://youtu.be/xoftn_EWOz8). These fragments were, as with the previous experiments, placed on the long-stalked glands on the underside of the lamina of two-month-old specimens of *B. filifolia* and *B. rorida*, both of which were close to anthesis, a one-month-old specimen of *B. guehoi*, flowering specimens of *B. liniflora*, *B. pilbarana*, and *B. rorida*, and a two-month-old seedling of *B. gigantea*. Fragments were also placed on the pedicel of a flowering *B. rorida* specimen, and the stem of the *B. guehoi* specimen. These specimens and species were chosen on account of being grown indoors (the annual species in an illuminated terrarium, and *B. gigantea* on an illuminated shelf) so that they were accessible for the purposes of creating a time-lapse video over periods of many hours. In the case of the *B. rorida* pedicel, the specimen was chosen because it was flowering at an opportune moment, and because the stalks on the pedicel were relatively long compared to those of *B. filifolia* (which was flowering contemporaneously in the author's collection), making the *B. rorida* pedicel a suitable subject for video observation.

Results and discussion

The observations conducted for the purposes of this article provide clear evidence of motile traps in all currently recognized *Byblis* species. The fragments of organic matter containing animal proteins (including the cheese, fish food, bloodworm, and the body parts of dead flies) which were placed on the stalked glands were almost invariably brought into direct contact with the leaf surface over a period of 2 to 24 hours (see, for example, the progress of the insect wing on glands of *B. liniflora* (Fig. 4). Stalked glands on pedicels and stems were observed to react in the same manner. The time-lapse videos unequivocally demonstrate that the transportation of the fragments towards the leaf surface is primarily achieved by a process whereby the stalks of glands whose gland heads are in contact with the fragments suffer a rapid loss of turgidity, causing them to collapse adaxially (i.e. in the direction of the leaf surface). The stalks of the pedicels and stems were observed to react in an identical manner. These findings support a reassessment of Darwin's categorization of the traps of *Byblis* as non-motile. Moreover, *Byblis* may be the only genus of carnivorous plant in which the stems and pedicels engage in active carnivory. The results also suggest that *Byblis* are able to differentiate between fragments which contain animal proteins and those which do not, for the latter are only very rarely transported to the leaf surface. This suggests that the stalk collapse is induced chemonastically (Fleischmann, pers. comm.).



Figure 4: Cultivated *Byblis liniflora* with insect wing. These photos show the progress of the wing towards the leaf surface.

Details of the process of motile trapping function in *Byblis*

The decision to use time-lapse video photography was motivated by the results from the set of experiments which involved intermittent observations without video technology. As well as showing fragments which had been brought into contact with the digestive secretions on the leaf surface, these intermittent observations revealed an earlier part of the process, when fragments had been drawn part of the way to the leaf surface but were not enveloped in a pool of fluid. This suggested that capillary action was probably not primarily responsible for drawing the fragments towards the digestive glands and raised a strong suspicion of a motile trapping process. The time-lapse video photography provides conclusive evidence of stalk movement in response to the capture of organic matter containing animal proteins. The videos (https://youtu.be/xofn_EWOz8) show that glandular reaction usually begins within a period of approximately two hours, although it can commence within mere minutes or only after several hours have elapsed. Movement of the stalks can usually be observed to be directly preceded by secretions from the digestive glands around the base of the affected stalked glands. Next, the stalks appear to collapse towards the leaf axis, drawing the fragment towards the leaf surface. Once in close proximity to the digestive glands on the leaf surface, the fragment makes contact with the pooled digestive secretions, and the resulting capillary action appears to accelerate the final part of the process. Depending on the size and weight of the food fragment and the species of *Byblis*, one to four hours were usually required until contact with the leaf surface. After contact occurs, the fragment is enveloped for many hours or longer by the fluid secreted by the digestive glands. Again, the process appeared to be identical for stalks on the pedicels and stems.

Given that there is no perceptible increase in the secretions from the stalked glands during the motile phase (which, if present, would suggest that the collapse is caused by movement of fluid from the stalk cells to the stalked glands (Fleischmann, pers. comm.)), it would seem to be the case that, upon stimulation by prey, fluid contained in the stalk cells passes into reservoir cells positioned at the base of the respective stalk cell, thus causing the collapse of the latter. It is perhaps pertinent to mention that Lloyd (1942, p 97) notes that each stalked cell “stands on a group of basal cells which may be as many as eight in number”. It may be that these basal cells serve as reservoirs to facilitate the collapse of the stalk cells. Should this explanation be correct, the process of motile trapping outlined here would appear to rely on communication between the stalked glands and the stalk cells, reservoir cells and sessile glands (Fleischmann, pers. comm.).

The movement of the stalks is, when observed through a time-lapse video, jerky rather than uniform. Food fragments that are in contact with more than one stalked gland are often twisted and partially rotated as they are moved. When a fragment is adhered to a single long-stalked gland, the stalk can be seen to flatten, and the fragment performs multiple 360-degree rotations as it travels towards the leaf surface. This suggests that the stalks rotate in a spiralfirm manner as they collapse. Interestingly, Lloyd (1942, p 97) describes how, when a stalked gland of *Byblis* “dries (in air or alcohol), the stalk cells twist.” Moreover, Darwin (1875, p 344) notes that the walls of these elongated cells are “marked with the most delicate spiral lines”, and that dried stalk cells are invariably found to be “spirally rolled up”. Fenner (1904), who studied the morphology of *B. gigantea* in detail, noted the spiral structure, and thought it an adaption “to allow bending of the [stalk] without collapse” (as translated by Lloyd (1942, p 97). But the observations conducted in connection with this work clearly show that the stalk cells do collapse, apparently permanently so. The presence of the spiral lines provides a convincing explanation for the spiralfirm collapse of the stalks that is evident in the time-lapse videos.

Stalk movement which conveys the fragments towards the leaf surface, or that of the pedicels or stalks, is only observed in stalks whose glands come into contact with the animal proteins. There is

no evidence of any reaction by stalked glands in the vicinity of those to which fragments are adhered which might serve to assist the latter in transporting the fragments. Observations made several hours after collapse of the selected stalked glands do, however, suggest that copious secretions from the digestive glands can precipitate further collapses of nearby stalked glands. But these collapses almost invariably occur once the fragment is in contact with the digestive secretions and play no role in transportation of the fragments. Motility, therefore, seems to be restricted to those glands that are in direct contact with the food fragments. It was also observed that the reaction of the stalks is much reduced or even absent in very old leaves and pedicels, and in plants grown in sub-optimal conditions.

Given the lack of any evidence that the stalked glands produce additional secretions in response to prey capture, it can be observed that the digestive glands appear to be solely responsible for all additional secretions which eventually envelop the fragments. Gradual reduction in the size of the organic fragments can be observed in the hours or even (usually in the case of the perennial species) days after contact with the secretions from the digestive glands, which is suggestive that digestive enzymes are present in these secretions. Additionally, it appears that, once a stalk cell has collapsed, it becomes spent, and does not regain its turgidity. This indicates that the process is connected to desiccation of the stalks and is quite unlike any motility exhibited by the traps of any other carnivorous plants (Fleischmann, pers. comm.). Certainly, observations made several days after apparent completion of the digestive process have provided no evidence of any restoration of the turgidity of the stalked glands. But, at least in the annual *B. filifolia*, *B. liniflora*, and *B. rorida*, the useful life of each leaf is little more than a month (Bourke, pers. comm., also the author's own observations on cultivated specimens). In these species, there would appear to be little cost benefit in cells possessing the ability to reset themselves for further carnivory. So, this trait might perhaps be particularly suited to the annual species, all of which exhibit rapid seasonal growth.

The results of the experiments conducted for the purpose of this article provide evidence as to why plants with access to insect prey can be seen frequently with dried prey attached to the leaf, pedicel, and stem surfaces. The ability of the stalked glands to collapse is very likely to improve the efficiency of the carnivorous syndrome in *Byblis* by bringing captured prey within range of the secretions of the sessile digestive glands. It would also seem reasonable to suppose that the motile abilities of the stalks may in many cases serve to bring captured prey into contact with other nearby stalked glands, thus enhancing the efficiency of the manner in which prey is ensnared (Rivadavia, pers. comm.). Nevertheless, the type of motile carnivorous trap outlined in this article may be regarded as rather simple compared to the far more sophisticated and strikingly different version practiced by *Drosera* (see generally Lloyd 1942). In particular, the stalks of *Byblis*, like those of other carnivorous Lamiales, but unlike those of carnivorous Caryophyllales such as *Drosera*, have no vascular bundles (Fleischmann *et al.* 2018; Lloyd 1942; Juniper *et al.* 1989), and cannot deliberately bend towards a chemical or other stimulus. The stalks of *Byblis* do not work in a coordinated manner, and observations suggest that an inconveniently placed leg or wing may prevent captured prey from being dragged into an optimal position for digestion and nutrient assimilation. It might, however, be noted that *Setocoris* bugs are likely to assist *Byblis* plants in sequestering nutrients from parts of the prey that remain outside of the range of the digestive fluids (Fleischmann, pers. comm.).

Evidence that motility in *Byblis* is triggered by detection of animal proteins rather than mechanical stimulation

Despite the generally simple nature of the motile trapping exhibited by *Byblis*, observations indicate that the plants may be able to detect, and react accordingly to, the capture of animal proteins.

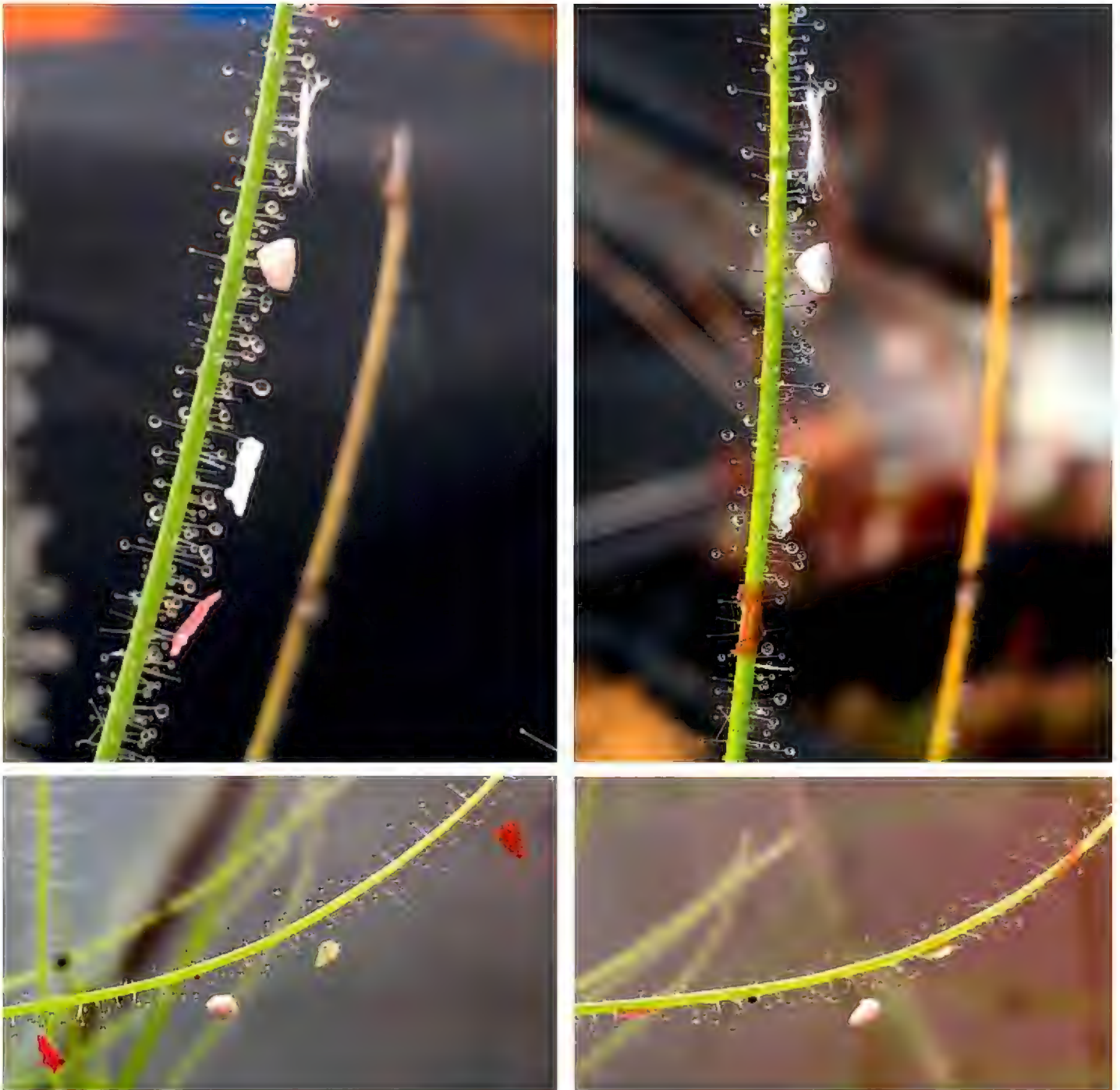


Figure 5: Top: Cultivated *Byblis gigantea* with (top to bottom) paper, perlite, cheese, and fish food adhered to stalked glands. Bottom: Cultivated *Byblis filifolia* with (left to right) fish food, perlite, fish food, and fish food adhered to stalked glands. Note how the perlite and paper show no signs of movement towards the leaf surface.

Unlike the fragments of animal proteins, similarly sized fragments of perlite and kitchen paper usually elicit no response from the stalks (see Fig. 5 top: *B. gigantea* with (from top to bottom of leaf) kitchen paper, perlite, cheese, and fish food; Fig. 5 bottom: *B. filifolia* with (from left to right of leaf) fish food, perlite, fish food, and fish food). This suggests that it is chemical rather than mechanical stimuli which provoke movement in *Byblis*. This effect is shown clearly by the results of the experiment conducted on *B. gigantea* and *B. lamellata*. None of the ten fragments of perlite or the ten of kitchen paper showed any evidence of movement, whilst the ten fragments of fish food all migrated to the leaf surface of the same plants. Of the ten fragments of cheese, eight had migrated to the leaf surface, whilst it was noted that both static fragments of cheese were positioned on the old leaves. Similar, albeit more casual, observations have been made on several occasions using the perennial species and also *B. filifolia*, *B. guehoi*, *B. liniflora*, *B. pilbarana*, and *B. rorida*.

It should, however, be noted that occasional observations, particularly on *B. filifolia*, *B. pilbarana*, and *B. rorida*, were made of perlite fragments having been transported to the leaf surface. These observations have virtually always been observed in respect of fragments of perlite placed in close proximity to fragments of organic matter containing animal proteins, and the reaction to the perlite was always far slower than the reaction to the organic fragments. It is here pertinent to recall the observations of the delayed collapse of stalk cells in the vicinity of copious secretions from the digestive glands. It is tentatively suggested that the occasional transport of the perlite to the leaf surface is a result of this latter phenomenon and does not represent a deliberate reaction to the capture of the inorganic material.

Interestingly, it has been observed that in nature, the collapse of stalked cells is not caused by the *Setocoris* bugs which often inhabit the plants as commensals (Bourke, pers. comm.). Similar observations have been made in cultivated specimens of *B. filifolia*, *B. gigantea*, *B. guehoi*, and *B. lamellata* which play host to *Setocoris* in the private collection of the author of this paper. This may be consistent with the notion that the stalk cell collapses occur primarily in response to detection by the stalked glands of chemical stimuli in captured animal proteins rather than to what is commonly referred to as a sense of touch.

Evidence of intra-specific differences in the process of active carnivory in *Byblis*

The observations conducted for this paper suggest that *B. aquatica* probably benefits very little, if at all, from its motile traps. This species, at least when beyond the seedling stage, produces extremely short stalks whose glands are furnished with relatively large droplets of mucilage. The secretions from the digestive glands (which are particularly copious), together with the large mucilage droplets from the stalked glands, are easily able, without any apparent need for stalk movement, to envelop materials which become adhered to the stalked glands (see Fig. 6). Indeed, in this respect, *B. aquatica* appears to employ a method of carnivory that superficially bears more similarity to that of *Drosophyllum* than to that of its fellow *Byblis* species (albeit that the precise mechanisms are not at all similar, because of the vascularization of the trapping organs in *Drosophyllum*). Perhaps notably, similar to *Drosophyllum* but unlike many if not all annual *Byblis* species, *B. aquatica* does not present stalked glands along the midrib (Bourke, pers. comm.).

The other species of *Byblis*, all of which have stalks which are much longer on average than those of *B. aquatica*, appear to be essentially uniform in their mode of carnivory. Some small differences were, however, observed. Insofar as the spiraliform stalk collapse is concerned, only partial rotations of the fragments can be observed in species with relatively short stalks, most notably *B. pilbarana*. This contrasts with longer-stalked species, such as *B. liniflora*, in which multiple 360-degree rotations always occur. The annual species of *Byblis* exhibit the most consistently rapid reactions, the prey usually being conveyed into contact with the leaf surface over a period of between two and six hours. The fastest reactions were observed in *B. rorida*, where stalk contraction can commence within a matter of minutes, and the entire process of transporting the fragment to the leaf surface can be completed within less than one hour of the placement of the fragment on the stalked gland. Intriguingly, *B. rorida*, has been shown by Laura Skates to be especially reliant, when compared to *B. filifolia*, *B. gigantea*, and *B. liniflora*, upon carnivory for obtaining nitrogen (Skates 2016).

With the perennial species, observation of the process is complicated somewhat by the overwhelming propensity of the glands to react only outside of daylight hours to the capture of prey. The process of drawing prey towards the leaf surface typically begins after sunset, and digestive fluid is almost exclusively secreted and re-absorbed overnight, so that, a few hours into the morning, unless the weather is particularly overcast, the glands are dry, and the prey is stuck fast to the surface of the



Figure 6: Cultivated (left) and wild (right, image courtesy of Andreas Fleishmann) *Byblis aquatica* showing very short stalks. Note the relative size of the pooled digestive fluid in the left photo.

leaf, stem, or pedicel. The process of secretion and absorption, if necessary, can be repeated over successive nights until the digestive process is complete.

Further research

It should be noted that since the observations explored in this paper were first made publicly available (via Facebook), horticulturalist and botanist Siggi Hartmeyer, has repeated the results in *B. liniflora* and *B. filifolia*, and in a hybrid between the two species (Hartmeyer & Hartmeyer 2019, p 74 this issue), capturing some extremely detailed video footage (<https://youtu.be/2hoUCQjf2LE>) of the cellular collapse. Hartmeyer also observed the phenomenon in a young *B. aquatica* plant, but he noted that in this species, the motile ability of the stalk cells was weak, and was unable to convey even a small fragment of fish food to the leaf surface without the assistance of gravity (pers. comm.). This supports the suggestions in this paper that the mechanism of carnivory in *B. aquatica* differs from that employed by other species in the genus. Another skilled cultivator of *Byblis* in the United States of America, Anthony Bell, has also observed the apparent transportation of flake fish food from the outer stalked glands to the leaf surface in *B. gigantea* (pers. comm.).

There is much scope for future investigations into the carnivorous syndrome in this under-studied genus. In particular, further research is required into the means by which the plants detect matter that is suitable for digestion and the factors which cause the stalk cells to collapse. It would also be very useful to investigate the manner in which the cells in the stalked glands, stalk cells, and digestive glands communicate with one another and co-ordinate their response to prey capture. A very fruitful avenue for further research would be to insert dye into the stalk cells to determine the

direction of the fluid diffusion which causes the collapses (Fleischmann, pers. comm.). The precise type of carnivory employed by *B. aquatica*, and its relationship in this respect with other species within the genus, should also be the subject of future studies, as should investigation into whether there is any correlation between the speed of the reaction of the stalked glands in particular species and the extent of their reliance upon carnivory for nutrient sequestration. It would also be potentially fruitful to assess the motility of the traps throughout the life cycles of various species. Finally, of course, it would be of great benefit if other horticulturalists, and in particular those with access to wild populations of *Byblis*, could seek to repeat the results outlined in this paper.

Conclusion

The observations in this article provide convincing evidence that *Byblis* ought no longer to be regarded as a genus of carnivorous plants with non-motile traps. Upon coming into contact with suitable prey, the stalk cells of the leaves, stems, and pedicels collapse inwards in a spiral motion, thus drawing prey towards the digestive glands and within range of the digestive secretions. This, it is submitted, provides strong evidence that all currently described members of the genus *Byblis* possess motile adhesive traps and should henceforth be treated as “active carnivores”.

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NOCTURNAL AND DIURNAL DIGESTIVE RESPONSES IN *BYBLIS GIGANTEA*, *DROSOPHYLLUM LUSITANICUM*, AND *RORIDULA GORGONIAS*

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Introduction

Byblis Salisb. is a highly understudied carnivorous genus currently consisting of eight recognized species – now with motile adhesive traps (Allan 2019 [p 51 this issue])). In particular, the carnivorous syndrome exhibited by the genus is imperfectly understood when compared to other carnivorous plant genera. The leaves, stems, pedicels, and sepals bear stalked glands and digestive glands. The stalked glands vary in length, even within individual plants, the longest stalks reaching 2.6 mm in length (McPherson 2010). Each stalked gland bears a droplet of mucilage, assumed to be sugar-based and water-soluble (Bauer *et al.* 2018), that is responsible for prey-capture. The far more numerous digestive glands sit in rows in longitudinal grooves on the epidermis (Lloyd 1942) (see Fig. 1) and are usually assumed to secrete digestive fluids in response to prey-capture, as well as to absorb the products of digestion (Cross *et al.* 2018). The stalked glands are capable of collapsing in response to detection of animal proteins, apparently due to a rapid loss of cell turgidity. In consequence, prey can be brought within the range of the secretions of the digestive glands.

Of the eight *Byblis* species, *B. gigantea* Lindl. and *B. lamellata* Conran & Lowrie, are perennials with very limited ranges in coastal Western Australia. *B. gigantea* inhabits sandy, nutrient-poor, winter-wet substrate in the Swan River drainage area, whilst *B. lamellata* is found in well-drained sandy heathland between approximately 100 km and 300 km north of Perth (Lowrie 2013). Both perennial species experience a Mediterranean climate with hot and sunny weather for large parts of the year, and both are generally in active growth for at least some of the warmer months (Lowrie 2013 and pers. comm). *B. gigantea* is the representative of the genus that was investigated for the purposes of this experiment (Fig. 2). The other six species are annuals from north-



Figure 1: Closeup of *Byblis gigantea* leaf showing rows of digestive glands (photo by Alexander Fisch).



Figure 2: A cultivated *Byblis gigantea*.

ern regions of Australia (and in the case of at least one species, the island of New Guinea), where they experience tropical and semi-arid climates (Lowrie 2013).

Published studies into the reaction of perennial *Byblis* to the capture of animal proteins are few and contradictory. Over a century ago, Bruce (1905) demonstrated that *B. gigantea* appears to be able to digest egg albumen, but that digestion is only evident when the albumen is placed in direct contact with the digestive glands. At around the same time, Fenner (1904) reported that the digestive glands produce copious secretions upon contact with prey, and that these glands appear dry after a period of four to six hours. But Lloyd (1942) applied carmine fibrin to the glands of *B. gigantea* and, over a period of two weeks, reported no evidence of digestion. More recently, Skates (2016) demonstrated, through stable isotope techniques, that wild *B. gigantea* obtained 31% of their nitrogen from prey (a smaller proportion than that found in the annual species tested). She did not, however, publish any findings as to whether the nitrogen had been sequestered directly through the actions of the plants' digestive secretions, or indirectly via excretions of *Setocoris* bugs that commonly inhabit *Byblis* species (although her research into the carnivorous syndrome is ongoing, and likely to yield very significant results). Thus, Lloyd's 1942 observations remain the most recently published research into the reaction of perennial *Byblis* digestive glands to contact with animal proteins.

More detailed research has in recent years been conducted into the production of enzymes by the annual species, also with inconsistent results. Hartmeyer (1997) concluded that the annual *B. liniflora* Salisb. does not produce proteases when it did not digest the gelatine layer of strips of photography film which were attached to the leaves 12 hours after the application of a 10% solution of yeast in water. When tested in the same manner, eight species, and one hybrid, of *Drosera* yielded positive results. Hartmeyer's findings, perhaps coupled with Lloyd's aforementioned failure to detect digestion in *B. gigantea* and the frequent presence on wild *Byblis* of *Setocoris* bugs which might act as commensals, precipitated doubts as to the ability of the entire *Byblis* genus (Hartmeyer 1998) or just the perennial species (Panaw *et al.* 2017) to produce digestive enzymes. Later experiments with film strips, however, have shown evidence of protease production by the digestive glands of another annual, *B. filifolia* Planch. (Hartmeyer 2005). A similar film-strip test with *B. liniflora* which was conducted in 2019 by this author also seemed to yield positive results (see below discussion). It has also been shown that phosphatase is produced by the digestive glands of *B. liniflora* (Płachno *et al.* 2005). Thus, the entire genus is now usually treated as able to produce its own digestive enzymes (Cross *et al.* 2018). Probably the absence of perennial species from these interesting investigations is attributable to their scarcity in collections worldwide; seed of perennial species can be difficult to obtain and hard to germinate, whilst living plants are only extremely rarely offered for sale.

My own personal observations over a period of several years were also initially mystifying. I have grown *B. gigantea* in a greenhouse in Birmingham, United Kingdom, since 2011, and *B. lamellata* in the same location since 2015. The greenhouse is heated in the winter, remaining frost-free. Plants are unshaded, and are exposed to full sun year-round, although supplemental lighting is used between November and March. For some time, however, I was perplexed as to whether observable digestive fluids are secreted by the plants. I routinely observed freshly captured prey adhered to the stalked glands, as well as older prey items which were bone-dry and stuck fast (to the extent they were difficult to dislodge) to the surfaces of the leaves (and sometimes the pedicels and stems) (Fig. 3). Despite close and repeated scrutiny, however, I was unable to observe any evidence of prey being in contact with digestive fluids. Prey appeared to be bone-dry at all times. Part of this puzzle has been solved by the recent discovery that the stalked glands are able to collapse upon contact with prey so as to convey the latter towards the digestive glands. But this motility does not explain how prey becomes stuck to the epidermis as a bone-dry husk.

It was observations of plants at night in my greenhouse which prompted the experiments that were conducted for the purposes of this article. On numerous occasions in summer 2013, I observed for the first time, under torch light, prey that was in contact with the surfaces of the leaves, pedicels, and stems of *B. gigantea*, and was enveloped in fluid which appeared to have been secreted by the digestive glands (see Fig. 4). The following day, by mid-morning, these prey items were virtually always bone-dry and stuck fast to the epidermis. Observations over following nights suggested that digestive secretions are sometimes secreted around the same prey items over successive nights. I also observed that fragments of bloodworm, flake fish food, and cheese have a similar effect, whilst fragments of paper and perlite elicit no response from the digestive glands. Indeed, fragments of cheese frequently cause such excessive digestive secretions that they literally drip down the leaf for many hours after the secretions have ceased and the cheese itself is dry. I have made similar causal observations on *B. lamellata* (see Fig. 5). This led me to hypothesize that the digestive glands of perennial *Byblis* species may secrete fluids almost exclusively during the hours of darkness. A basic film-strip test of the kind used by Hartmeyer yielded results which suggest that these fluids contain proteases. Tiny fragments of cheese were used to stimulate digestion, and the film strips were placed on top of the site of digestion for several days, secured with paper clips (see Fig. 6). Similar experiments on *Drosophyllum lusitanicum* and various *Drosera* species also produced positive results, whilst results on *Roridula gorgonias*, and on film strips with similarly-sized fragments of cheese and a few drops of water, were entirely negative.

Interestingly, I also applied the film-strip test to *B. liniflora* in March 2019. A very small fragment of bloodworm was placed on the underside of the leaf, and film-strips were placed both on the upper and lower surfaces of the leaf (so that the leaf with the bloodworm fragment was sandwiched between the two film strips) and secured with a paperclip. After a period of 20 hours, the film-strips were removed and the result appeared to be strongly positive (see Fig. 6) (although it should be noted that the leaf in question had withered by the end of the period – not an uncommon occurrence when the leaves of young annual *Byblis* are over-stimulated by bloodworm). It should be noted also that, over a similar time period, a film strip upon which a fragment of bloodworm was placed and wetted with several drops of water did not show any evidence of digestion of the gelatine layer. Unfortunately, at the time, I only had one young plant available, and the tests could not be repeated. Hartmeyer's tests on *B. liniflora* (1997) involved stimulating the digestive glands with 10% yeast solution several hours prior to applying the film-strips. It is possible that any digestion of the solution was completed by the time that he applied the film-strips, so that the sessile glands had ceased their secretions, and were not stimulated by the gelatine on the film (although Hartmeyer (2005) found that *B. filifolia* protease release apparently was triggered by the gelatine, albeit quite weakly compared to various *Drosera* species). Certainly, the least that can be said is that all species of *Byblis* would benefit from further investigations using film-strip tests.



Figure 3: Prey stuck fast to the leaf surfaces of a cultivated *Byblis gigantea* plant.



Figure 4: A night time shot of a fly's head enveloped in digestive secretions whilst an adult *Setocoris bibliophilus* lurks on a leaf in the background.



Figure 5: *Byblis lamellata* photographed soon after sunrise showing clear evidence of digestive secretions which were released nocturnally around the cheese. By the time that this photograph was taken, the digestive secretions had ceased, and the excess digestive secretions (often stimulated by cheese fragments) have started to drip down the leaf. Such secretions are gradually re-absorbed.

The purpose of the experiments which are summarized in this article was to investigate the hypothesis regarding nocturnal secretion of digestive fluids. The other subjects of this experiment were *Drosophyllum lusitanicum* L. and *Roridula gorgonias* Planch. The carnivorous *D. lusitanicum* is the only extant representative of the genus *Drosophyllum* L. It inhabits dry coastal areas in southwestern Spain, Portugal, and northern Morocco, where it experiences a Mediterranean climate (McPherson 2010) that is similar to that in which perennial *Byblis* (especially *B. lamellata*) are found (Brewer *et al.* 2018; Paniw *et al.* 2017). *Drosophyllum* is the sole extant genus within the family Drosophyllaceae and belongs to the order Nepenthes. It is thus unrelated to *Byblis*, which is the sole extant genus within the family Byblidaceae and belongs to the order Lamiales (Fleischmann *et al.* 2018). Perhaps unsurprisingly, *Drosophyllum*'s carnivorous syndrome is fundamentally different from that of *Byblis* because, unlike those of the former, its stalked and sessile glands are vascularized (Lloyd 1942). Accordingly, its stalked glands produce constant secretions of mucilage (Darwin 1875), although the digestive glands release secretions only in response to prey capture (Darwin 1875; Lloyd 1942). *Drosophyllum* nevertheless exhibits several superficial similarities to *Byblis*. Although it is a passive adhesive carnivore, it shares with *Byblis* the character of producing stalked glands which are primarily responsible for prey-capture, and sessile glands which perform the functions of digestion and absorption. In neither *Drosophyllum* nor *Byblis* are the leaves able to move in response to the capture of prey. This can be contrasted with *Drosera*, a genus which has sophisticated stalked glands (true tentacles (Bartosch *et al.* 2018)) which are able to work in co-ordination to secure prey



Figure 6: Film-strip test in progress on *B. gigantea* (left); film-strip results for perennial *Byblis* (top right) and *B. liniflora* (bottom right).

ties, indicative of convergent evolution (Poppinga *et al.* 2018), suggested that there might also have been value in ascertaining whether *Drosophyllum* produces digestive fluids primarily at night time. Notably, although *Drosophyllum* has been subject to far more rigorous research than has *Byblis*, there is, to date, no published research which investigates the nocturnal and diurnal responses of its digestive glands.

Roridula gorgonias L. is one of two perennial species which comprise the genus *Roridula* L., both of which are carnivorous. *Roridula* is the extant sole genus in the family Roridulaceae, of the order Ericales (Fleischmann *et al.* 2018). *Roridula* is thus more closely related to Sarracenaceae than to Byblidaceae or Drosophyllaceae. Both *Roridula* species exhibit passive adhesive traps which utilize stalked glands to capture prey. Although *R. gorgonias* inhabits substrates which are wet year-round (Cross *et al.* 2018; Alexander Dietrick pers. comm.), it experiences a climate that is roughly similar to that of the perennial *Byblis* and of *Drosophyllum* (McPherson 2010). Crucially, however, the stalks covering the leaves of *Roridula* produce resinous droplets, within which enzymes cannot operate (Bauer *et al.* 2018). It has no sessile glands and does not produce digestive secretions of proteases. Digestion is instead accomplished predominantly through commensal bugs from the genus *Pameridea* (Bauer *et al.* 2018). *Roridula* was adjudged to be an ideal subject for these experiments because its proven lack of digestive secretions would suggest that, if the animal matter placed on its leaf surfaces remained dry throughout the experiments, any moisture observed on the animal matter placed on the

and optimize digestion, and also has (in many species) leaves which possess the ability to deploy movement to aid in the process of carnivory. (Darwin 1875; McPherson 2010). Moreover, both *Drosophyllum* and the perennial *Byblis* are similar in basic appearance, producing fili-form leaves 20 cm or more in length which radiate from central stems (see Fig. 7) that periodically die off and are replaced with new growth so that each individual plant may eventually produce several growth points. These superficial similarities,



Figure 7: A cultivated *Drosophyllum lusitanicum* plant.

glands of *Drosophyllum* or *Byblis* could reasonably be attributed to the digestive secretions rather than to the products of condensation, or to fluid secreted by the animal matter.

Methods and Materials

The experiments here described consisted of placing fragments of dried bloodworm in such a position that they were in direct contact with the leaf surfaces of cultivated specimens of *Byblis gigantea*, *Drosophyllum lusitanicum*, and *Roridula gorgonias*. The fragments were observed at various intervals over several consecutive 24-hour periods in order to ascertain at what time of day (if any) digestive activities took place. The subject plants were all growing in a greenhouse in Birmingham, UK, in full exposure to sun. The greenhouse door was open at all times. Five plants were used: one *B. gigantea* that was in flower; one sub-adult *B. gigantea* that was due to flower within the next two or so months; one seedling of *B. gigantea* that was approximately five months old; one *Drosophyllum* that was several years old and had flowered a few months previously; and one *R. gorgonias* that was in flower. Two fragments were placed on separate leaves of each plant.

Results

The results are set out in the table below:

Table 1.															
Day	1	1	2	2	2	3	3	3	4	4	4	5	5	5	6
Observation Time	D	E	N	D	E	N	D	E	N	D**	E	N	D	E	N
<i>Drosophyllum</i> fragment 1	A	+	++++	-	-	+++	-	-	-	-	-	-	-	-	-
<i>Drosophyllum</i> fragment 2	A	+	++++	-	-	-	-	-	-	-	-	-	-	-	-
<i>R. gorgonias</i> fragment 1	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>R. gorgonias</i> fragment 2	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>B. gigantea</i> seedling fragment 1	A	-	++	-	++	+++	-	-	+++	++++	-	++	-	-	-
<i>B. gigantea</i> seedling fragment 2	A	-	++	-	++	-*	-	-	-	+	-	-	-	-	-
<i>B. gigantea</i> sub-adult fragment 1	A	-	+++	-	++	+++	-	-	-	+	-	-	-	-	-
<i>B. gigantea</i> sub-adult fragment 2	A	-	+++	-	++	++	-	-	++	+	-	-	-	-	-
<i>B. gigantea</i> flowering plant fragment 1	A	-	+++	-	++	+++	-	-	+++	+	-	-	-	-	-
<i>B. gigantea</i> flowering plant fragment 2	A	-	+++	-	++	+++	-	-	-	-	-	-	-	-	-

Key

Days: 1= 29 July; 2= 30 July; 3= 31 July; 4= 1 August; 5= 2 August; 6= 3 August

Observation time:

D = day (observation made between 10:00 and 14:00)

E = evening (observation made between 18:00 and 20:30)

N = night time (observation made between 00:00 and 02:00)

Note that sunrise at this time of year is approximately 05:30, and sunset is approximately 21:00.

Observation of glandular activity

A = fragment of bloodworm added

- = no glandular activity apparent

+ = slight glandular activity present (bloodworm wet where in contact with epidermis)

++ = significant glandular activity present (bloodworm saturated and/or secretions from surrounding sessile glands beginning to pool on epidermis)

+++ = copious glandular activity present (bloodworm saturated and significant pooling of secretions from sessile glands on epidermis)

++++ = extremely copious glandular activity present (bloodworm saturated and extreme pooling of secretions from sessile glands on epidermis)

*The bloodworm was not visible from this point onwards. It may have been entirely digested.

**This was a very wet and overcast day.

The fragments were observed for glandular activity between 29 July 2016, when they were added, and 3 August 2016, when the observations ceased. Observations were made during the day time (between 10:00 and 14:00 BST), evening (between 18:00 and 20:30), and night (between 00:00 and 02:00). Sunrise at this time of year in Birmingham, where the experiments were conducted, is approximately 05:30, and sunset is approximately 21:00. The surprising results of these experiments prompted similar observations of the reaction of a specimen of *Drosera slackii* to bloodworm fragments over a period of several days.

A similar experiment was conducted on a specimen of *Drosera slackii* grown in identical conditions as the plants in the table above showed a very different response. A fragment of bloodworm was added at 11:45, and already by 13:45, copious secretions were being produced while the tentacles and leaf had bent over, smothering the bloodworm. This process continued, apparently unaffected by daylight and darkness, for a 24-hour period, after which the remnants of the bloodworm began to dry out, and no further evidence of digestive secretions could be perceived.

Discussion

These results suggest a clear propensity in *B. gigantea*, and also in *Drosophyllum*, to release digestive secretions, and to absorb the products of digestion, outside of daylight hours. *R. gorgonias*, as expected, demonstrated no reaction to the bloodworm fragments. In particular, it should be noted that the bloodworm fragment appeared bone-dry and stuck fast to the epidermis of *B. gigantea* during the periods in which no glandular activity could be perceived. The results also suggest that *B. gigantea* and *Drosophyllum* (but particularly the former) may repeat the process of nocturnal digestion and absorption for each prey item over several successive nights. The aforementioned causal observations of *B. lamellata* suggest that this perennial species displays a similar propensity. Casual observations on trapped prey over a period of several years are consistent with the results obtained

from these experiments. Contrarily, the digestive processes of *Drosera slackii* appear to be entirely unaffected by daylight, even strong sun, when grown in a greenhouse alongside *Drosophyllum* and the perennial *Byblis*. Notably, similar, albeit more casual, observations have been made in *D. binata*, *D. regia*, and *D. capensis*.

It is interesting to note that whilst the bloodworms on *B. gigantea* and *Drosophyllum* were observed to be enveloped in digestive fluid during the hours of darkness, and neighboring glands were seen producing secretions, there was no comparable night-time increase in secretions from unstimulated digestive glands positioned elsewhere on the subject plants. This corroborates the aforementioned findings in previous publications indicating that the digestive glands of *Drosophyllum* and probably *B. gigantea* secrete only in response to prey-capture, and do not produce secretions on a continual basis. In particular, the extent to which the bloodworm fragments were stuck fast to the epidermis of *B. gigantea* plants during daylight hours suggests that the digestive glands entirely cease to secrete at such times, rather than secreting continuously and merely losing fluids via evaporation during the daytime. Furthermore, the lack of significant observable nocturnal glandular secretions from digestive glands which were not in contact with animal proteins provide clear evidence that the digestive glands of both *Drosophyllum* and *Byblis* do not secrete indiscriminately during the hours of darkness. Rather, the observations derived from these experiments provide strong evidence of a deliberate and localized strategy of nocturnal digestive processes in *Byblis* and *Drosophyllum*.

These observations would also appear to rule out hygroscopy (i.e. the ability to absorb water from air humidity) as the primary explanation for the phenomenon of virtually exclusive nocturnal digestion. The mucilage secreted by the stalked glands of *Drosophyllum* has been described as “greatly hygroscopic” (Adamec *et al.* 2009, p 3), so it is by no means unlikely that the digestive fluids possess hygroscopic properties. But, if this is so, whilst hygroscopy might provide a partial explanation for the large quantities of liquid observed at night, it seemingly cannot account for the fact that the prey items usually appear to be completely dry during the day time.

These results raise several searching questions, which I hope will be the subject of further research. First and foremost, it would be desirable for wild plants to be investigated in order to confirm whether the phenomenon of nocturnal digestion also occurs in their natural habitat. An obvious question which requires further research is whether it is darkness or another factor (such as increased nocturnal humidity) that prompts the nocturnal secretion of digestive fluid from the digestive glands. Although there was evidence of such secretions on the very overcast morning on day four of the experiments, the greenhouse in such weather conditions was both darker and more humid than on the brighter days of the experiment. Casual experiments on perennial *Byblis* plants placed indoors where temperatures and humidity are more or less constant, but which still appeared to produce secretions from the digestive glands only when in darkness, suggest that lack of light might be the key factor. However, the digestive secretions appear to be more copious in plants which remain in the (more humid) greenhouse at night, suggesting that increased nocturnal humidity may play a role in stimulating the enzymatic secretions by the leaves. It may also be that in these conditions the digestive fluids are augmented in volume by the effects of hygroscopy - although it should be reiterated that the fact that the secretions are concentrated around the prey at night and usually absent altogether during the day seems to rule out hygroscopy as the primary explanation for these nocturnal fluid increases.

The annual *Byblis* species should also be investigated to ascertain the extent to which they manifest similar digestive behaviour. Casual observations on terrarium-grown and greenhouse-grown specimens suggest that they do, but in a manner significantly less pronounced than their

perennial counterparts. In particular, it can often be observed that in bright light, annual *Byblis* species usually secrete some digestive fluids soon after animal proteins become adhered to the stalked glands, as is evident from some of the time-lapse videos described in Allan (2019 [p 51 this issue]) (in particular those of *B. liniflora* and *B. rorida*). By way of comparison, the time-lapse video of motility in *B. gigantea*, recorded in good light, shows no evidence whatsoever of digestive secretions. But it can also frequently be observed in all annual species that the volume of fluid enveloping preys greatly increases during hours of darkness, and that this cycle can be repeated over several 24-hour periods. Whether increased nocturnal secretions in the annual species are caused by low light levels or higher nocturnal humidity, and the extent to which hygroscopy plays a role, is currently unclear.

Another question is why the carnivorous cycles of perennial *Byblis* and *Drosophyllum* have adapted in this manner. It might tentatively be suggested that the tendency towards nocturnal digestive and absorptive activity may be an adaption to the harsh natural climate that *Drosophyllum* and the perennial *Byblis* inhabit. Both may be found in active growth in very hot and dry conditions with relatively low humidity. Indeed, the surface of the sandy substrate which is inhabited by both species of perennial *Byblis* when in active growth may become sufficiently hot to fry an egg (Allen Lowrie, pers. comm.). But the precise reason for this apparent adaption remains elusive. A possible answer is that secretion of digestive fluids in the hot and sunny summer conditions experienced by *Drosophyllum* and the perennial *Byblis* would be likely to lead to much costly evaporative loss, an affliction that would be almost entirely avoided by secretion during the hours of darkness. This is certainly an aspect which warrants further research.

Conclusion

The research conducted for the purposes of this article suggest that *B. gigantea* and *Drosophyllum* (and probably also *B. lamellata*) secrete digestive fluids, and absorb the products of digestion, primarily during the hours of darkness. This phenomenon, which is suggestive of a hitherto unrecognized level of sophistication in the carnivorous syndrome, has not previously been reported in either genus, or indeed in any other carnivorous plants. Further research, however, is needed in order to verify this phenomenon, and to discover its causes and the precise purpose which it serves.

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OBSERVATIONS AND TESTS ON CULTIVATED TROPICAL *BYBLIS*

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Introduction

The annual *Byblis* species (Byblidaceae, Lamiales) are predominantly Australian endemics with *B. liniflora* extending also north to Papua New Guinea (Cross *et al.* 2018). Beside their features as sticky carnivorous plants, many enthusiasts especially appreciate their bushy appearance with many showy hermaphroditic flowers. The following report features our experiences with the cultivation and hybridization of *B. filifolia* and *B. liniflora* over two decades at our heated greenhouse in Weil am Rhein (Germany).

Soil, germination, and growing conditions

During several field trips in northern Australia (1990-2001), we encountered many *Byblis* in the tropical wetlands, often growing in almost pure silica sand or various sand-laterite mixes mostly under full sunlight. Frequently, the plants occurred together with different large spider leg sundews (*Drosera* section *Arachnopus*). Due to the successful cultivation of these sundews in our heated greenhouse over years, we decided to keep our *Byblis* species the same way. Our standard soil for that purpose was a mix of high-quality peat (source Thomas Carow, Germany) with 25-35% lime-free silica sand (0.4-1.2 mm grain size) and about 10-15% perlite or alternatively 5 mm pumice granules. However, this is just one possibility that worked fine for us, probably also other peat-sand mixes may do it. Beware of too high amounts of or even pure sand, which is dangerous because the pots dry out very quickly in the sun, which may be fatal for the plants. On the other hand, we experienced *B. liniflora* growing nicely from a dropped seed in a thin carpet of algae on the side wall of the water bowl in which the actual pots were standing (Fig. 1). It flowered and set seeds for a whole season with its roots just growing into the pure water.



Figure 1: *Byblis liniflora* rooting in a carpet of algae and water without soil (left). A potted *B. liniflora* fed with *Drosophila* (right).

For our experiments on enzyme production (2007) and hybridization (2011), we treated most seeds for 24 hours with an 0.1% aqueous solution of gibberellic acid (GA3) to increase germination rate. Indeed, these seeds germinated after only 5-7 days, which is very fast. However, during the following seasons we found out that fresh *Byblis* seeds (directly sown or from the former season) germinated quite nicely even without any special treatment. Therefore, we meanwhile forego the GA3 treatment for fresh seeds, even if germination may take a week or two longer.

Very important for a good germination and growth are high temperatures between 25-40°C, which are usual summer day temperatures in our greenhouse. From October to April, we added 400-watt HQI lamps to provide sufficient light and additional heating during winter; however, the best growth always occurred when we sowed the seeds in March/April so the plants could grow up under full sun during the hot season.

Nutrition is another important point to get healthy and rapidly growing *Byblis*. We usually feed *Byblis* and *Drosera* seedlings first with crushed fish food flakes, using magnifying tweezers. Do not give too much at once, to avoid mold or even rotting leaves. As soon as the plants reach a size sufficient to capture fruit flies (*Drosophila*), this diet is recommended. If you have enough seedlings, it is an interesting test to leave some of them unfed. Even after a few weeks, the difference between fed and unfed plants is unambiguous. As an alternative to manual feeding, which may be time consuming if you have numerous plants, we tried fertilizing the plants. In 2018, we placed a ball (about a teaspoon of pearls) of Osmocote (16% N, 7.5% P₂O₅, 9% K₂O) 5 cm above the bottom of a 15 cm pot with *B. filifolia* and kept several plants without Osmocote in the usual 9 cm pots. The difference in growth speed and date of flowering was remarkable. Especially eye-catching was the strong branching of the fertilized *B. filifolia*, one reason for their bushy appearance. The unfertilized plants produced no branches and fewer flowers at a later time (Fig. 2 left). The different pot sizes were certainly not essential for the different growth during this experiment. However, every coin has two sides: One of the branched plants developed a fasciation (Fig. 2 right) and all fertilized plants withered in late autumn 2018. But two of the unfertilized plants are now, at the end of February 2019, still alive, even if unbranched and much less impressive.



Figure 2: Left: Contemporary *B. filifolia* grown from the same seed batch. Slender unbranching, flowerless unfertilized plants on the left and bushy, strongly branched, flowering plants fertilized with Osmocote on the right. Right: Fasciated *B. filifolia* fertilized with Osmocote.

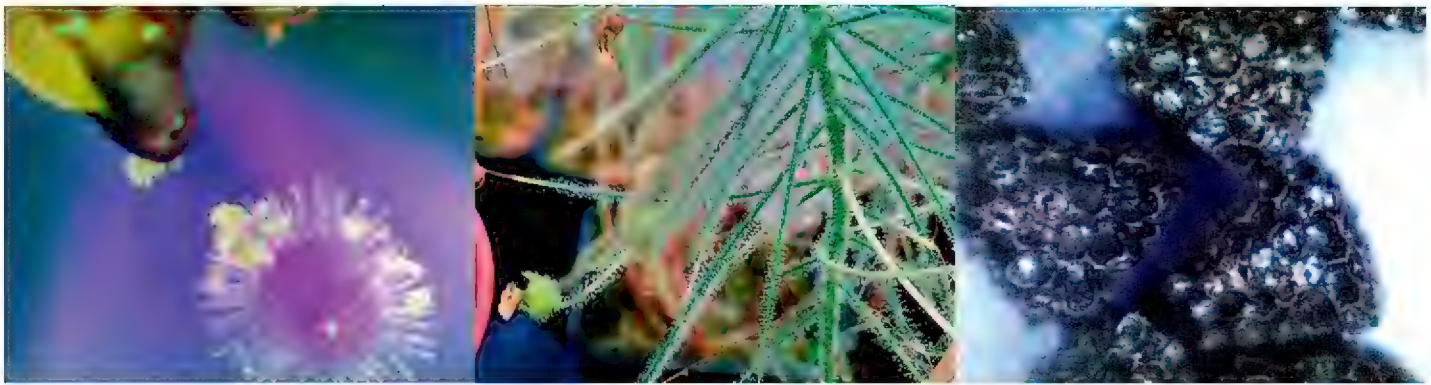


Figure 3: Anthers and stigma of a self-pollinating *B. liniflora* (left). *B. filifolia* seedpod with ripening hybrid seeds (center). *B. filifolia* x *liniflora* F1-seeds (right).

Pollination and hybridization

It may be difficult to successfully pollinate *Byblis* flowers and obtain seeds. However, you just need to know how to do this properly. The easiest are self-pollinating species like *B. liniflora*, where everything works automatically: flowers self-fertilize, seed pods swell, dry out, open, and release healthy seeds only a few weeks after flowering. However, other species like *B. filifolia* depend on a so-called buzz-pollination where, in nature, pollen is only released by the buzzing wings of pollinating insects. A simple method to release such *Byblis* pollen in cultivation is to imitate the buzz either with a tuning fork or with the tip of an electrical tooth brush (without brush attachment). Just hold a piece of paper below a flower to collect the released pollen and hold the “buzzer” close to the yellow anthers. Now you can pollinate other flowers quite easily.

In 2010, we tried to produce a *Byblis* hybrid at our greenhouse (Hartmeyer & Hartmeyer 2011), although we could not find any literature on such natural or artificially produced hybrids. We took the whole flower of a self-pollinating (non-branching) *B. liniflora* with visibly released pollen (Fig. 3) and rubbed it directly on the flower of an only buzz-pollinating large branching *B. filifolia*. To our great delight, we saw a seedpod developing that actually released healthy looking seeds after some weeks. To avoid any errors, we repeated the procedure and once again a seedpod developed and released healthy looking seeds (Fig. 3).

We immediately sowed the seeds and had a really happy day when they started germinating some weeks later. The final result was a branching and self-pollinating plant that reached a size intermediate between the parent plants (Fig. 4).

Enzyme production

In 1997, we conducted several enzyme tests with photo film (based on the digestible gelatin layer) on different carnivorous plants



Figure 4: *B. filifolia* x *liniflora* “F1-hybrid” herbarium sheet (2011).

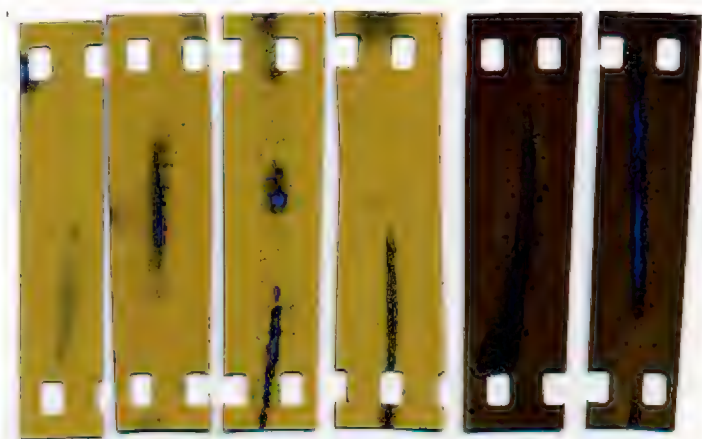


Figure 5: Six-fold enzyme tests with photo film (gelatin layer) on *B. filifolia* (2005).

became clearly visible on the photo film. We repeated the test and obtained the same result. As such, *Byblis* was rehabilitated as a true carnivorous plant genus, able to produce its own digestive enzymes. Comparing the necessary time to achieve unambiguous results on the gelatin layer (~2 days *Drosera*, ~6 days *Byblis*) enabled an admittedly rough assessment of their digestive capacity. Accordingly, *Byblis filifolia* attains an estimated 20-40% of the “average *Drosera* digestive capacity” (Fig. 5).

(Hartmeyer 1997) and found no clear enzyme evidence for a self-pollinating *B. liniflora* that we had grown for several years at that time. For different *Drosera*, the enzyme tests were always unambiguous after only 1-3 days, but that was actually not sufficient for *Byblis*. In 2005, we repeated the enzyme test particularly for a large branching *B. filifolia* (Hartmeyer & Hartmeyer 2005); however, we extended the usual test period from three to six days. And indeed, after three days, first enzyme caused patterns emerged in the gelatin layer, and after six days the typical holes

Discussion

During three decades of cultivating tropical *Byblis* in a greenhouse, we can state that the plants tolerate various permanently wet peat-sand-mixes and may grow even in almost pure water. For rapid and healthy growth, the plants need nutrition, either by existing insect prey, by manual feeding, or alternatively from a soil fertilizer like Osmocote. A hybridization was successful with *B. liniflora* pollen on *B. filifolia*; however, we recommend to try even other combinations. This is certainly an interesting topic for future experiments. The conducted photo film (gelatin) tests finally confirmed that *Byblis* is in fact carnivorous, able to produce their own digestive enzymes.

In late 2018, the Byblidaceae again attracted particular attention regarding their prey capture due to thrilling time lapse videos by Dr. Gregory Allan (GB) on Facebook, clearly showing a movement of the sticky hairs. Darwin wrote that he had never heard of motile unicellular structures (Darwin 1875). The trichome stalks of *Byblis* are unicellular, so he regarded *Byblis* traps as non-motile. Even later observations that the trichomes move down to the leaf surface after contact with prey (Lloyd 1942) did not prompt further experiments, just like the more or less permanent leaf and pedicel movement by pulvini (Barnes 2009; Hartmeyer & Hartmeyer 2010). Gregory Allan’s amazing videos (Allan 2019, p 51 this issue) encouraged us to conduct our own experiments with *B. aquatica*, *B. filifolia*, *B. liniflora*, and the hybrid. Our results fully confirmed the observation that *Byblis* trichomes are able to move after prey capture; documented in a video posted on YouTube (Hartmeyer & Hartmeyer 2018).

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BYBLIS IN CULTIVATION IN THE TROPICS AND IN TEMPERATE CLIMATES

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This article has been written based mostly on the authors' experiences in growing *Byblis* in the UK and in Singapore. It is hoped that growers in regions with different climates will be able to extrapolate from the information provided here, adjusting the methods described below to suit their own growing conditions. Hopefully much of the information provided here is universal in its application.

Introduction

If any genus of carnivorous plants deserves to be better known, both by horticulturalists and botanists, it is *Byblis*. The common name (ironically rarely used by enthusiasts) for the genus is “rainbow plants”, on account of the prismatic effect that can be produced when the sun shines on their copiously-produced sticky glands. All species follow a basic morphological plan: they have a central stem from which radiate numerous filiform leaves and scapes with showy flowers that typically have purple petals (although white forms of most species are known) and vivid yellow anthers. Virtually all parts of the plants are covered in mucilage-tipped stalked glands (colloquially referred to as “tentacles”), which efficiently capture small insects, as well as microscopic sessile digestive glands. Another interesting characteristic of the genus is the presence of pulvini in most, if not all, species. Pulvini are swellings at the base of pedicels which, usually after successful pollination, utilize hydraulics to bend the pedicel, and consequently the developing fruit, downwards towards the ground. This phenomenon was discovered by Brian Barnes in the early 21st century.

From the time of Charles Darwin until the late 20th century, *Byblis* were classified as passive carnivores. However, towards the end of the century, doubts emerged as to whether *Byblis* were able to produce digestive enzymes at all, and they frequently came to be regarded as merely protocarnivorous plants. Subsequent tests conducted during the first part of the 21st century did demonstrate enzyme production and nutrient sequestration, confirming *Byblis* as a true carnivore. The most recent research suggests that *Byblis* tentacles collapse inwards in response to prey capture, which indicates that they ought to be regarded as active carnivores. In nature, all species have been observed to play host to bugs from the genus *Setocoris*, which feed on the plants' ensnared prey without becoming trapped by the sticky glands. It is also strongly suspected that *Byblis* spp. obtain nutrition indirectly via the *Setocoris* bugs in a manner similar to *Roridula* and their commensal *Pameridea* bugs.

The species of *Byblis*

All *Byblis* species inhabit Australia, although one or more have also been recorded from the southern tip of the island of New Guinea. All grow in very nutrient-poor habitats which are subject to regular wildfires. They are commonly found sympatric with various *Drosera* and *Utricularia* species and, in Australia's Cape York Peninsula and New Guinea, *Nepenthes*. Two *Byblis* species are perennials, whilst the other six are annuals.

The perennial species: *Byblis gigantea* and *B. lamellata*

Byblis gigantea is listed on the IUCN Red List as critically endangered and is found in a handful of sites within the Perth metropolitan area (which has predictably unfortunate implications for

its conservation) plus a few sites in the adjacent Darling Range. *Byblis lamellata* inhabits a small area approximately 275 km north of Perth. Both species are found in nutrient-poor substrates consisting entirely or primarily of sand, often growing alongside tuberous and pygmy *Drosera* species. The perennial *Byblis* are bushy plants, very similar in appearance, producing leaves that can exceed 25 cm in length, with stout stems reaching more than 40 cm in height that often branch, and bearing beautiful flowers which are several cm in diameter and usually have deep purple petals. Healthy adult specimens are a magnificent sight (Fig. 1). Seedlings produce increasingly long leaves prior to stem-production, until they superficially resemble large (unrelated) *Drosera filiformis* plants. In nature, plants produce foliage from autumn onwards, dying back during mid to late summer. Re-growth from the roots, or leaf axils on spent stems, occurs when cooler and damper conditions return, occasionally after wild fires have depleted competing plants. *Byblis gigantea* is actually slightly smaller than *B. lamellata*, and inhabits conditions that are rather wetter, particularly during the southern Western Australian wet season. Indeed, at least climatically, and in respect to its well-drained nutrient-poor substrate, the habitat of *B. lamellata* has been described as resembling somewhat that of *Drosophyllum lusitanicum*. Although there are also significant differences between the habitats of these two unrelated species, it is useful from a horticultural perspective to note that they grow well side by side in similar substrate with a similar watering regime.



Figure 1: *Byblis gigantea*.

The annual *Byblis* species

All annual *Byblis* are endemic to monsoon tropical to semi-arid regions of northern Australia plus southern New Guinea. Germination occurs as the wet season commences (often after fires) and the reproductive cycle is completed before seasonal dry conditions prevail. Anther length compared with filament length has been a useful characteristic to identify different *Byblis* species. However, in the absence of flowers, tentacle length at the mid sections of leaves can also be useful (see Table 1). More in-depth studies are needed to verify whether the three characters described in Table 1 are reliable and stable characters across the variation found in annual *Byblis* taxa.

The following is a general introduction to each recognized species, and a description of each as they generally appear in cultivation (as opposed to a technical discussion of taxonomy):

Byblis aquatica

This species is usually reported as growing in areas which, throughout the wet season, become inundated so that adult plants grow in several cm of water, although inundation is not necessary in cultivation. In cultivated forms, the leaves are usually 2-3 cm in length and furnished with extremely short tentacles. Some forms are robust with a stem that is self-supporting up to at least 10 cm in length, whilst other forms are more delicate in appearance. Unlike most species (but in common with *B. liniflora*), the anthers are shorter than the filaments. Although the flowers are small, the

Table 1. Comparison of <i>Byblis</i> tentacles at the mid sections of leaves, observed on the 6 annual species grown at the same time under identical conditions in Singapore.			
Species	Tentacle density	Tentacle length	Size of mucilage drops
<i>Byblis aquatica</i>	Sparse	Uniformly similar in length, maybe the shortest among the six species	Largest of all six species
<i>Byblis guehoi</i>	Dense	Varied lengths, the longest up to 4× the length of the shortest	Varies between forms, but never as large as in <i>B. rorida</i>
<i>Byblis filifolia</i>	Dense	Varied lengths, but not as long nor as varied as in <i>B. guehoi</i>	Varies between forms but never as large as in <i>B. rorida</i>
<i>Byblis liniflora</i>	Dense	2-3 different lengths but not as varied as in <i>B. filifolia</i>	Larger than in <i>B. pilbarana</i> but smaller than in <i>B. rorida</i>
<i>Byblis rorida</i>	Denser than in <i>B. aquatica</i> but not as dense as <i>B. liniflora</i>	2-3 different lengths but not as varied as in <i>B. filifolia</i>	Large, but still smaller than in <i>B. aquatica</i>
<i>Byblis pilbarana</i>	Dense	2-3 different lengths and similar to <i>B. liniflora</i>	Smallest of all

leaves can become reddish-purple in some forms, and the short tentacles with comparatively large mucilage droplets make for very beautiful plants, somewhat resembling frosted Christmas trees.

Byblis filifolia

A very variable species which inhabits areas that are seasonally damp but rarely inundated (as do all annual species other than *B. aquatica*). All forms produce large and showy flowers bearing anthers that are longer than (or at least equal in length to) the filaments - a characteristic shared with *B. guehoi*, *B. pilbarana*, and *B. rorida*. The most wonderful forms hail from the Pago region (Kimberley, Western Australia), reaching at least 60 cm in height with stout self-supporting stems, as well as leaves that can exceed 20 cm in length. The stems can form branches, often with several growing points bearing numerous flowers simultaneously (Fig. 2). Other forms, including the rather inaptly-named *B. ‘Goliath’* (a cultivar of *B. filifolia*), produce long but straggly stems and shorter leaves rarely exceeding 10 cm in length.

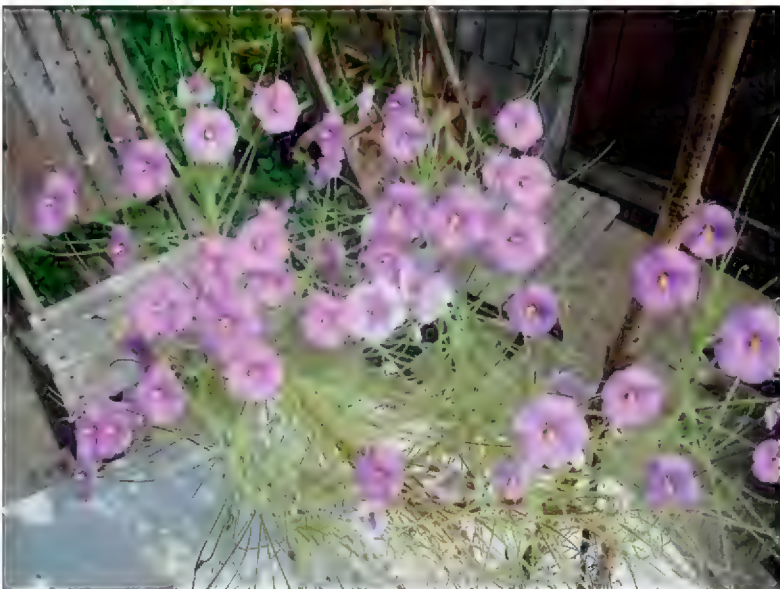


Figure 2: A single plant of the giant form of *Byblis filifolia* originating from the Pago Region, Kimberley, Western Australia.

Byblis guehoi

This is surely one of the most spectacular of all carnivorous plants. Although rather similar in basic appearance to the shorter-leaved forms of *B. filifolia*, this species, when grown well, has stems which branch profusely. Individual plants can have dozens of growth points and more than 70 flowers open simultaneously. (Fig. 3)

Byblis liniflora

This widespread species is compact and densely covered in sticky glands. It has relatively small but pretty flowers, only a few of which usually open at any one time. The anthers are shorter than the filaments (a characteristic shared with *B. aquatica*).

Byblis pilbarana

Recently described, this species originates from the vicinity of the Great Sandy Desert in the Pilbara region of Western Australia, one of the hottest in all of Australia. On the basis of photographs taken on a field trip by Professor Hans Lambers, it seems that the range of the genus, probably represented by *B. pilbarana*, extends several hundred kilometers inland into the Karlamilyi National Park. Very delicate in appearance, its pedicels (flower stalks) are much longer than the leaves and tend to point skywards (Front Cover). Interestingly, specimens in habitat tend to have stocky stems with short internodes, whilst most cultivated specimens seem to become lanky over time.

Byblis rorida

This species is similar to the short-leaved forms of *B. filifolia*, but the growing point is covered in dewy sessile glands which, unlike the digestive glands, are clearly visible to the naked eye. The function of these dewy sessile glands is unknown. The beautiful flowers often have deeply serrated edges (Front Cover). There is a giant form originating from Lawrence, Dampier Peninsula, Kimberley, Western Australia, which has short internodes and can become quite bushy in appearance.

Cultivation

Perennial species

Getting started: Owing to the scarcity of plants for sale and to their delicate nature (not shipping well), most growers start with seeds. Fire often stimulates germination in nature, so GA3 treatment is recommended for germination in cultivation (GA3-free germination in cultivation is virtually unknown). We recommend a 4-5-day soak in GA3 (conc. 500 ppm), although smoke discs have been reported to be just as effective. Do-it-yourself fire-treatment is another option, but we find this method is unreliable and can result in much wastage of good seed.

Germination can take place in as little as 14 days. Seedlings initially develop very slowly and are very susceptible to damp-off. Survival rates are best when germinating under lights indoors (but



Figure 3: *Byblis guehoi* dominating a summer greenhouse. Also present in the picture are *B. gigantea*, *B. lamellata*, and *B. filifolia*, as well as several other species of carnivorous plants.

not in a terrarium), although satisfactory results can be obtained in temperate regions in spring in a sunny greenhouse (and presumably on a very sunny windowsill or in a conservatory).

The perennial species are extremely difficult to grow in places such as Singapore where the ambient humidity is consistently high. Even seedlings that are placed at open and well-ventilated areas are excessively prone to dying off soon after germination, especially during monsoon season. To date, we are not aware of any growers who have successfully cultivated perennial *Byblis* to flowering size in the tropics, even though some have tried using air conditioners to lower the ambient humidity and temperature.

Substrate: An airy, sandy substrate is required, approximately 3:2:1 ratio of perlite : lime-free sand : moss peat works well for plants of all ages. The proportion of perlite can be increased. Sand may inhibit the ability of the roots of some seedlings to penetrate the surface of the substrate. Seedlings should be transplanted into pots 10 cm or so deep, but very carefully since they have surprisingly long and fine roots. Plantlets over ~12 cm in height should be transplanted carefully into pots at least 20 cm deep. Adult plants appreciate a 1 cm top-layer of pure sand.

General conditions: Full sun is required, ideally in frost-free greenhouses, conservatories or south-facing windowsills (north-facing in the Southern Hemisphere) to replicate their Mediterranean climate. In temperate climates, plants should be overwintered indoors or in a heated greenhouse, preferably under lights. Stems will become increasingly yellowish and straggly over winter. For more information regarding long-term cultivation indoors under lights, refer to Anthony Bell's article in this same issue. Sometimes, an especially vigorous plant will sprout shoots from the base before the main stem is mature (Fig. 4).

Watering: Rainwater is preferred since hard tap water may kill plants. Seedlings and young plants can take very wet conditions. Adult plants can be watered through a tray system. Prior to replenishing, allow the tray to dry, especially in winter (it matters less in summer). Ideally, when plants are grown in the recommended deep pots, the topmost layer of sand on the soil surface should remain bone dry at all times, whilst the substrate below should remain damp.

Propagation: Best by seed. Flowers must be hand-pollinated with pollen from a genetically distinct individual. Vigorously (but gently) brushing the anthers will stimulate the release of pollen, which can then be transferred to the stigma of other flowers. A tuning fork is often said to be necessary to achieve pollen release, but a toothpick or similar item works equally well. Successful pollination will result in swollen fruit which eventually dries out. They must be pried open, since dried fruit will not open on their own in cultivation. Stem and root cuttings have also been reported to work.

Things to avoid: The primary challenge of growing perennial *Byblis* in the UK lies in getting the plants through our dark damp winters. Tall pots, airy substrate, and as much light as possible are the key factors for success. The following are to be avoided:

- Sodden substrate (especially around the crown).



Figure 4: An especially healthy *Byblis lamellata* sprouting shoots from its base when the main stem is still young (courtesy of Anthony Bell).

- Heavy substrate containing too much peat (the traditionally-recommended peat and sand mix is, in the longer term, a death sentence).
- Hard tap water.
- Lack of light, especially in humid winter conditions.
- Excessive heat, or freezing temperatures, in winter.
- Repotting in late summer, autumn, or winter - and careless repotting which breaks the long and very fragile roots.

Pests:

- Seedlings and young plants are very susceptible to attack from slugs and snails.
- Aphids can infest plants during the winter.
- Mealy bugs around the base of the stems, which can easily be removed by hand.

Feeding: Plants with limited access to prey seem to appreciate the application of bloodworm or flake fish food to the leaves. The leaves of very young plants can be killed by the application of too much food, especially bloodworms. It also pays to be aware that old or excess food may encourage fungal growth. Plants grown in greenhouses or outdoors usually catch an abundance of prey without intervention. Some growers have reported success with fertilizers, either by fertilizing the substrate with Osmocote, or by spraying the plants with a foliar feed such as MaxSea.

Annual species

Getting started: Again, most growers start from seed. All species (except *B. liniflora*) require GA3 or smoke treatment for reliable germination. A 1-2-day soak (500 ppm) will suffice. Bleach treatment is sometimes recommended, its benefits are unproven. All species inhabit very warm climates and grow in full sun. Therefore, it is best to germinate seeds in a heated and well-lit terrarium or propagator for growers outside of tropical regions.

Feeding: Lack of nutrition usually results in weak specimens. Very vigorous plants can be produced when frequently fed with crushed flake fish food, which can be sprinkled onto the tentacles once the leaves are 1 cm or so in length, or fragments of bloodworm. Leaves of young plants can wither if overfed, especially with bloodworm, but the latter can stimulate especially good growth. Plants grown outdoors in the tropics, or in greenhouses in other regions, usually catch plenty of prey of their own. Some growers have reported great benefit in using fertilizers. For example, Paul Young in England gave two *B. aquatica* plants weekly sprays of MaxSea, with spectacular results (Fig. 5). Steven Jones in Hawaii, and Siggi Hartmeyer in Germany, amongst others, have also demonstrated that pellets of Osmocote in the substrate can be of great benefit to the plants.

Watering: In temperate regions, all species are happy sitting in a cm or so of water at all times. Once adults, they are also very tolerant of quite dry spells. It has, how-

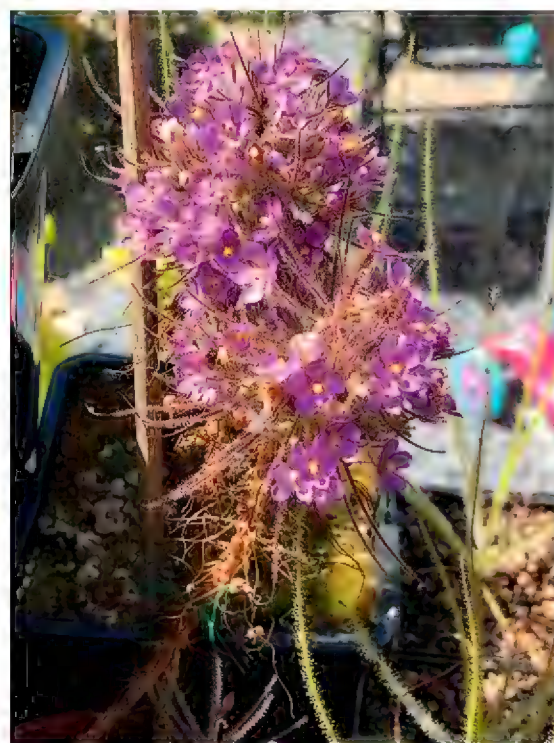


Figure 5: Two very robust and floriferous specimens of *Byblis aquatica* growing side-by-side. This spectacular growth seems to have resulted from regular foliar fertilization. The plants both produced great numbers of very short branches, each of which bore several flowers (courtesy of Paul Young), possibly a result of intense fertilization.

ever, been observed by tropical growers that soaking wet media resulting from the tray system possibly leads to fasciation of adult *B. guehoi* and *B. filifolia*, especially when small pots (10 cm or less) are used.

Where to grow them: In Singapore (and other areas with a similar climate, at least in the summer), the annuals grow well in full sun (protected from torrential rains) or at a sunny east or west-facing windowsill. Seedlings can be transplanted and placed into ambient conditions soon after germination as long as the media is kept moist. However, *B. aquatica* seedlings seem to appreciate much higher surrounding humidity until they are about 3 cm tall. Afterwards, the seedlings can be transplanted into their own pots and grown together with the rest of the annual species with several hours of direct sunlight outdoors or at the windowsill. In temperate regions, smaller species can be kept in heated terraria year-round, whilst the larger species will outgrow all but the largest terraria.

Species-specific guidance

***Byblis aquatica*:** Grows best in a 3:2 mix of perlite : moss peat mix or 1:1 of perlite : LFS or live sphagnum. If well-fed, it can do well even in very shallow substrates (large plants can be obtained in only 2 cm of soil). In the UK, it is best kept for its entire life-cycle in a heated terrarium, although it will survive for several months in a summer greenhouse. It is self-fertile but will not usually produce seed without the anthers being teased. Inundated conditions are not required in cultivation.

***Byblis filifolia* and *B. guehoi*:** The aim should be to induce plants to produce branches from the leaf axils (Fig. 6), which usually appear contemporaneously with the first flower-buds, resulting in huge and profusely-flowering specimens. A 3:1:1 substrate of perlite : moss peat : household compost for acidic plants works well. The extra nutrients of the compost appear to encourage branching. Very vigorous plants can also be obtained using a 3:2 substrate of perlite : LFS or live sphagnum, as long as the plants are well-fed.

To give *B. filifolia* and *B. guehoi* time to reach their full potential in temperate regions, it is best to germinate seeds in a terrarium or propagator in late winter or early spring. Frequent feeding with fish food and or bloodworms will result in vigorous plants which, in central England, can be placed in a greenhouse from the beginning of June, or a sunny windowsill a month earlier (Fig. 7). Large plants require 20 cm deep pots for the best long-term growth,



Figure 6: *Byblis guehoi* starting to produce side branches.



Figure 7: A single *Byblis guehoi* plant on a south-facing windowsill in summer, Birmingham, UK.

although they can attain flowering size and set seed in small pots. They can be germinated in small peat pots, then, once larger, be placed inside deeper pots. To obtain seed, flowers must usually be cross-pollinated in the manner described for the perennial species. Adult plants are quite cold-tolerant, surviving in England until mid-October in an unheated greenhouse, or until Christmas on a windowsill. They eventually become increasingly straggly until they are finished off by the short photoperiod. As a general benchmark for growers from regions with different climates, the average high in June in central England is around 19°C, and the average low is around 10°C.

In tropical regions, the best time to sow seeds of these species is during the coolest and/or wettest month of the year (December in Singapore). Plants will flourish for about 10 months, after which they grow too tall and lanky. Most growers in Singapore use 100% LFS or 1:1 mix of perlite : LFS in large pots to encourage vigorous branching and thus spectacular plants.

***Byblis liniflora*, *B. pilbarana*, and *B. rorida*:** These species will do well in a 3:2 mix of perlite : peat, or 4:2:1 of perlite : sand : peat, or even 1:1 of perlite : LFS or live sphagnum. They do best in pots at least 10 cm deep. *B. liniflora* is self-fertile and often produces copious amounts of freely germinating seed. *B. pilbarana* and *B. rorida* must be cross-pollinated in the manner described for the perennial species. They do not usually produce copious amounts of seed, so they need to be pollinated attentively. All three species will be fine on a windowsill or in an unheated greenhouse from June onwards in central England, but they tend to die well before *B. filifolia* and *B. guehoi*.

Propagation by cuttings: When mature plants start looking straggly, stem cuttings of about 6-8 cm can be taken using pair of sharp scissors. These portions of stem can be stuck into 100% loosely packed LFS or 1:1 ratio of perlite : LFS or even 100% perlite, leaving about 2/3 of the stem above the media (Fig. 8). The cuttings should be placed in a very bright area or under artificial lighting where the humidity can be kept constant at about 50-70%. When kept warm (25-28°C), stem cuttings will produce roots within a week or two (Fig. 9). New side shoots usually emerge from the decapitated mother plant and continue their life cycle as if nothing had happened, sending out new flowers eventually (Fig. 10). With younger plants, cutting the main stem may cause it to turn brown and die. Maybe because of its thin stems, *B. pilbarana* doesn't seem to appreciate being propagated in this manner, but more tests need to be conducted on this relatively new species to find out if stem cuttings can be a dependable method of propagation.

Things to avoid:

- In terraria, plants do not like being too close to grow lights (perhaps due to excessively low humidity). However, if there is glass between the lights and the



Figure 8: Stem cuttings of *Byblis guehoi* in 100% perlite.



Figure 9: Roots of *Byblis guehoi* cutting in 100% perlite.

growing space, they enjoy being very close to the lights.

- Plants struggle in heavy substrate containing too much peat. The traditionally-recommended peat and sand mix gives very poor results.
- Hard tap water.
- Lack of light - the annual species grow in bright tropical sun.
- Frequent repotting. Seedlings can be carefully transplanted from seed trays to larger pots, but avoid repotting mature plants.
- Inbreeding amongst the non-self-fertile species. This can lead to infertile plants or a poor seed set, but can be averted by maintaining several plants of each species and carefully crossing them. Swapping seed with other growers is perhaps the most effective way to avoid inbreeding.

Pests: Seedlings and young plants are very susceptible to slug and snail attacks. Adults plants can be attacked by various pests when reaching the end of their life cycles, but, at least in temperate regions, adult plants are not susceptible to pests when in their prime. Adult plants are very prone to mealy bugs when grown in overly hot and humid conditions, especially after the flowering season. Sometimes the infestation can be so bad that the whole plant may be killed.

Byblis Hybrids

In Singapore, *B. filifolia* ‘Goliath’ was successfully crossed with *B. guehoi* in September 2011, the latter being the pollen donor. Germination rate was >80% and the F1 hybrids were fertile and varied in characteristics: some were more like *B. ‘Goliath’* (very tall, less branching) while others were more like *B. guehoi* (more compact, heavy branching). No further generations were raised, so this is certainly an area for future experimentation. The presence of hybrids between the annual species in the wild has not been reported. Hybrids between the perennial species have been reported in cultivation.

Setocoris

These fascinating insects inhabit all *Byblis* species in nature. They possess the amazing ability to crawl up and down the sticky glandular surfaces with virtual impunity, and they feed on insects captured by the plants. It is suspected that their droppings provide the plants with additional nourishment. The best-known of species of this little-studied genus is *Setocoris bybliphilus*, which inhabits *B. gigantea*. Juvenile *S. bybliphilus* bugs superficially resemble greenfly in color and shape. The short-lived adults are superficially similar in appearance to ants (Fig. 11). Allen Lowrie claims that the perennial species are better adapted to accommodate their resident *Setocoris*, since their leaves lack stalked glands on the upper surfaces, apparently providing convenient pathways for *Setocoris*

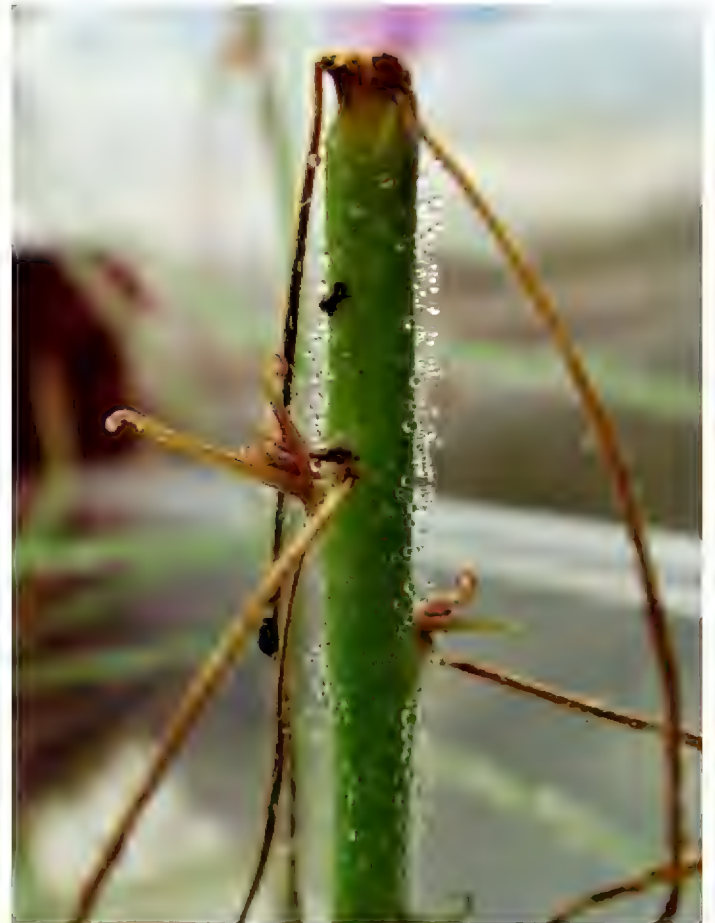


Figure 10: Side shoot produced on stem cutting of *Byblis guehoi*.

to traverse the leaves and leave droppings for the plants' benefit. *Setocoris* are very easy to keep and breed, simply living on greenhouse-cultivated plants year-round. Many of them die during the winter, presumably having laid eggs on the plants, since the population usually explodes again in spring. At this time, they spread rapidly to any annual *Byblis* growing nearby, and also to neighboring *Pinguicula*, *Drosophyllum*, and some *Drosera* (e.g. *D. regia*). Pesticides must be avoided at all costs – winter problems with greenfly on perennial species seem to be the price of keeping these fascinating and little-studied insects.



Figure 11: *Setocoris bybliphilus* on *Byblis* (courtesy of Stéphane Joly).

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Suggested reading for the *Byblis* enthusiasts:

- Bourke, G., and Nunn, R. 2012. Australian Carnivorous Plants. Redfern Natural History Productions. Poole, Dorset, England: 1-197. [Contains numerous rare shots of various *Byblis* species in habitat.]
- Lowrie, A. 2013. Carnivorous Plants of Australia Magnum Opus, Volume 1. Redfern Natural History Productions. Poole, Dorset, England: 1-458. [As well as numerous habitat photos and specific sections on each species, there is also a section which covers *Setocoris* bugs.]
- McPherson, S. 2008. Glistening Carnivores, The Sticky-Leaved Insect-Eating Plants. Redfern Natural History Productions. Poole, Dorset, England: 1-392. [An excellent summary of the genus.]
- McPherson, S. 2010. Carnivorous Plants and their Habitats, Volume 2. Redfern Natural History Productions. Poole, Dorset, England: 725-1442. [Contains a summary of the genus very similar to that in McPherson's 2008 text (above).]

PERENNIAL *BYBLIS* INDOOR CULTIVATION

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Byblis gigantea is a carnivorous plant that resides in parts of Western Australia and has been listed as critically endangered in the IUCN Red List. I here describe my experiences cultivating this species indoors for the past two years. First of all, it can be done! Some may claim that it's impossible to keep both *B. gigantea* and *B. lamellata* indoors in a temperature-controlled environment, but I have been successful (see Back Cover) and would thus like to share my experiences. I do have a small greenhouse where I am currently attempting to grow perennial *Byblis* to see how well they hold up in the sweltering Texas heat that we often get here in the north-central part of the state. I believe I can do it with some minor adjustments, but in this article, I want to focus on indoor cultivation. Due to their spacing requirements, I had to set a lot of other carnivorous plants to the side in order to begin my project and eventually succeed at growing these plants. With a little understanding of what it takes to make them happy, it's not difficult at all.

To start, you may wish to submit seeds to "smoke treatment". It has been suggested that by doing this method, the seeds themselves are cued by a warm stratification and along with being introduced to organic compounds (butenolides) found in smoke named "Karrikins" (Chiwocha *et al.* 2009; Dixon & Roche 1996). Although I have performed this treatment many times and have had good luck in doing so, I simply prefer to soak the seeds in a solution of gibberellic acid, or GA3, as an 0.1% aqueous solution, for five days. This is a gibberellin pentacyclic diterpene acid that promotes the growth of cells and has many different effects on the development of plants. It also increases seed germination rates and is known to help *B. gigantea* seeds overcome dormancy. For further information regarding GA3, see Pavlis (2018). I've found that seeds that float are probably not viable, but I sow them anyway, just in case. After performing the GA3 soak, I sow seeds immediately and give them a little water using the tray method. I recommend placing a seed germination mat under the tray to provide a little warmth from the bottom of the tray.

My first *B. gigantea* seeds were purchased from a nursery in Czechoslovakia and were labeled *B. gigantea* "Perth Airport". I soaked the seeds in GA3 as described above, then sowed them. About a week later, I noticed I already had germination. I carefully watched over the next day or two for the others to follow. Promptly, the first two that sprouted succumbed to damping off fungus and the others never germinated. I began searching online and talking to as many people as I could but discovered that there is very little information available online about the cultivation of these wonderful plants and no one seemed to know much about it either. So, I purchased more seeds from all over the world, each time trying something different in how my setup is arranged, or a new growing technique.

When I first began this journey, I was sowing *Byblis* seeds in 3.5 liter pots full of medium, only to lose them to damping off fungus shortly after germination. Instead of trying to treat a huge pot of medium with fungicide (and crossing my fingers hoping I eradicated it), I would just throw all of the medium away, sterilize the pot, and then start over. It can become expensive and very time-consuming to continuously mix up new batches of medium if damping off keeps occurring! I then switched to sowing seeds in 5 cm peat pots (also known as Jiffy pots). A peat pot is a small biodegradable fiber container or pot that many hobbyists use to start seeds in. Worst case scenario, it's easier to discard both the peat pot and the seed or dead seedling. But if successful, you can simply transfer the whole peat pot into the final pot in which you choose to grow the plant in. The peat pot will eventually break down into the medium and dissolve over time. But be sure to rinse the peat

pots well with RO (reverse osmosis) or distilled water before use to remove salts. However, perennial *Byblis* naturally occur in places that are not totally devoid of all minerals, so no need to worry about a little buildup. My TDS (total dissolved solids) stays regularly between 20-50 parts per million, like a lot of my other carnivorous plants, and the *Byblis* are unphased by this.

Medium for both of the perennial *Byblis* species should consist of: 3:2:1 perlite:lime-free sand:peat moss. I often have to use pool filter sand, as a lot of the good stuff in my area is nowhere to be found. Using a fine hand sifter, get the smaller grains out and keep the larger ones. Be sure to rinse the medium well, continuously testing the runoff with your TDS meter. After everything is ready, take a rinsed 5 cm peat pot and fill it to the top with medium. Gently pack it down and place the treated perennial seed in the center, pressing very gently to ensure it stays put. You do not need to bury it.

I then place the peat pots in a 25×50 cm tray, adding water until the pots become saturated. But do not over-water, leaving it so that there is just enough water to keep the medium moist at the surface. I will attempt to water again the next day or so, to see if the pots will absorb any more water. If not, I will discard the water as opposed to letting it sit in the tray. Using a slight draft from nearby fans gives adequate ventilation to the seedlings and makes it difficult for any fungus to take hold. Run a fan as often as possible. In one of my rooms, a fan stays on day and night. Once the plants on that shelf mature past that vulnerable stage, I continue to leave the fan on, as I am already moving in new pots to germinate the next batch of seeds. This is a balancing act of keeping good air circulation, while not letting your medium dry out. It is also worthy to note that, as adults, neither of the perennials seem to like high humidity indoors. The type of artificial lighting that I have done well with varies. I germinate my seeds under dual bulb T8 fluorescent fixtures using a bulb of each 5000k and 6500k. A photoperiod of 16 hours on and 8 hours off worked well. I have also done well with T5-HO fluorescent bulbs.

After germination, to avoid damping off from excess humidity around the seedlings, take a pinch or two of dry sand and lightly sprinkle around the plants. This will help keep the area around them from becoming overly saturated with water. Be very gentle to avoid getting sand onto the plants, as it can be rather unsightly stuck to the mucilage. As the plants continue to grow, keep a fan gently blowing and add just enough water in the trays to keep the medium moist. Continue sprinkling dry sand in the immediate area surrounding the seedlings until eventually you no longer see peat moss. You can keep the edges of the pot free of sand to help assess the soil moisture with a finger. Once your plant is about 5 to 8 cm tall, you are just about in the clear. After transferring to the final pot, I cover the surface with dry sand for cosmetic purposes. I believe adding sand around the seedlings, coupled with constant air flow from the fans, are key to avoid damping off.

The roots of developing *B. gigantea* and *B. lamellata* elongate very quickly, so it is advisable to employ “Slack potting”, using the same medium as mentioned above in the external pot. Slack potting (Slack 1980) involves taking the peat pot that contains your seedling and placing this into a larger pot filled with media (Fig. 1). Slack potting minimizes root disturbance to the seedlings



Figure 1: Carefully concealing the peat pot into the permanent pot using dry sand.

and it also helps maintain a constant level of moisture throughout the medium surrounding the seedlings. Adrian Slack originally proposed this method for the cultivation of *Drosophyllum lusitanicum* and it can be used successfully for other types of plants too. Select a pot that is a minimum of 20 cm tall since it is harder to maintain constant moisture in smaller pots. The plants will show signs of stress if their roots don't have adequate room to grow and stretch out. I recommend mixing in a little Osmocote 15-9-12 in the medium of the larger pot. Before setting the peat pot into the 3.5 liter pot, I carefully cut the bottom of the peat pot off using a sharp razor. I then place the peat pot so that it is about 6 mm below the top rim of the large pot and fill in the rest with dry sand. This will conceal the peat pot and also give the plant a more natural look. My plants quickly reached maturity and flowered at approximately 7-8 months of age.

Perennial *Byblis* will stop sending up new leaves and flower stalks towards the end of the growing season, as they approach dormancy time. In nature this happens during the summer months, when growth rate will slow down significantly. For me, this occurs from late summer through fall, with plants waking up around early spring and actively flowering from around mid-March until around November. When growing indoors, dormancy is not a requirement and will not harm the plant if skipped. However, during this time I like to reduce watering and give them a little rest period by only supplying their watering trays with the amount of water that they will soak up in a few minutes. I then let the pots dry for a few days and repeat this procedure every week until the growing season approaches.

In preparation for spring, and to stimulate vigorous new growth, I take a pair of scissors and trim the leaves all the way back around mid-March, leaving only a couple of cm of the previous season's growth. It is important though to not trim back the leaves before spring, so the plants can keep photosynthesizing – and in case you wish to apply foliar feeding (yes, they will still appreciate feeding during their resting period!). However, if you're using Osmocote, as recommended above, feeding may not be necessary. After cutting the leaves back, you will soon notice new growth emerging and may even see new shoots from other sections of the rhizome, eventually growing into a very large plant.

I also repot my perennial *Byblis* around mid-March, at the same time that I trim the leaves. But I only repot if and when I see an excessive amount of roots protruding from the bottom of the pots, or if the plant appears to look quite large for its pot. When adults, they're fortunately not as sensitive to root disturbance as younger plants. During the repotting process, make sure to not let the roots dry out. Keep them moist at all times! Plants need to be transferred to their fresh substrate immediately after being pulled from the old medium. I recommend repotting once every two years, or every year in case you observe unsightly algae buildup on the soil surface. Algae buildup might be a sign that the plants are being kept too wet. You may trim and repot at the same time, but refrain from doing either during the growing season. With the appearance of new growth, you may also see flower scapes emerging. At this time, I recommend setting the tall pots into 2.5 cm of water every day for the duration of the growing season. Slightly moist medium will do nicely, but do not let the soil dry out during active growth. My plants flower from April to November.

By following the above tips, you will hopefully obtain healthy adult *B. gigantea* and *B. lamellata* that you will grow to love. If you maintain the plants properly by trimming and repotting, they will grow vigorously. You will know it is happy when it sends out an array of flowers that many plants could only wish they had!

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AN AMATEUR'S EXPERIENCES WITH *BYBLIS* GERMINATION

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Most carnivorous plant growers who've been in the game for at least a year or two tend to be passingly familiar with at least one of the several *Byblis* species currently described. *Byblis liniflora* in particular is a common weed, easy to germinate and easy to grow. The rest of the genus, however, presents a series of challenges to successful cultivation (and subsequent maturation), the first of which being successful germination of the seeds.

While *B. liniflora* often requires little more than a quick soak in water and then sowing on moist soil to germinate (though in this method it may take several weeks), the rest of the genus possesses distinctly fire-adapted seeds which require some form of special treatment in order to germinate. Among the options that cultivators have come up with: sowing on moist soils and lighting cool grass fires over the top, before pouring water into the ashes; treating with commercial smoke disks or "liquid smoke" applications for similar chemicals; soaking seeds in an approximately 10% bleach solution; and, perhaps most commonly now, treating seeds with a gibberellic acid (GA3) solution. In previous years I personally have had limited access to smoke products or viable GA3 (eBay sources are not always reliable for quality ingredients), and so have attempted several other options such as the grass fire (or variations thereof) and bleach treatments, settling mainly on the latter due to somewhat higher success.

More recently, however, I managed to acquire both viable GA3 powder as well as a number of *Byblis* species I had not had access to before, and saw an opportunity to conduct an experiment of my own on which method (bleach or GA3) is the most viable, particularly for a novice grower who may not readily have access to working chemicals.

Bleach Treatment

As bleach is a highly caustic chemical it is very important that this method is performed with care and hands are washed thoroughly after use. A proper solution for treatment is a dilution of approximately 10% household bleach to 90% pure water. Seeds should be placed in the solution and fully submerged with all sides exposed to the solution, and then carefully monitored. The bleach will remove a fair portion of the outer seed coat and the inhibitive chemicals held in it over a period of several minutes, turning the normally black seeds to a lighter shade of purple, brown, or gray; if you watch the seeds you will see a black or purplish trail or cloud seep out from the seed as it soaks. Seeds should be removed from the solution and rinsed as soon as a change in color becomes apparent; if they are left long enough to turn light gray or white, the whole seed coat has been removed or the bleach has penetrated all the way through and the embryo will be compromised.

Once fully rinsed, the seeds can then be sown in a pot on the proper soil (I personally use a sandy peat-based mix, sometimes topped with a very thin layer of milled sphagnum to help ward off mold and damping off), and germination of viable seeds should occur within 1-2 weeks.

GA3 Treatment

Treating seeds with GA3 is somewhat less touchy than the bleach method, and if spilled on the hands is less of a concern (though washing is still advised). *Byblis* seeds should be soaked in a concentration of approximately 1000 ppm, which can be achieved by dissolving approximately 100

Table 1. Germination of <i>Byblis</i> seed (number germinated of number sown).		
Species	Bleach Method	GA3 Method
<i>B. filifolia</i> “Pago Giant”	3 of 6	10 of 12
<i>B. filifolia</i> “Hidden Valley”	3 of 5	5 of 5
<i>B. rorida</i> “Lake Champion”	2 of 3	2 of 3
<i>B. guehoi</i>	3 of 5	5 of 5
<i>B. aquatica</i> “Robust Form”	1 of 5	3 of 5
<i>B. lamellata</i> × <i>gigantea</i>	0 of 4	4 of 4

mg of GA3 powder in 100 ml of water. Warm water is best, and full dissolution can be achieved by allowing the solution to sit overnight; dissolving the powder in a very small amount of warm ethanol or rubbing alcohol can also speed up the dilution process. Once the solution is prepared and all powder is visibly dissolved, annual *Byblis* species can be soaked for 24 hours before sowing, and the perennial species for 5-6 days. Then, seeds can be placed in pots in a similar regimen as in the bleach treatment. Germination should similarly occur anywhere between 4 days and about 3 weeks after.

Germination Results

The species/forms (Table 1) each had one group of seeds treated with bleach and one with GA3, with at least 3 seeds in each group (up to 12 seeds per group, determined by the number of seeds I had to work with for each).

Out of these, all test groups tended to have the first germination of seeds within 10 days of sowing, continuing up to approximately 4 weeks after sowing, so time until germination differed little between the two methods. This is where the similarities end, however.

For all but *B. rorida* “Lake Champion” (likely primarily due to the small number of seeds I had to work with for that form, only about 3 seeds per test group), GA3 treatment resulted in a higher germination rate (Table 1). Additionally, at first glance the GA3 germinated seedlings also appeared to be more robust than those germinated via the bleach method, and continued to be so as they’ve matured.

The *B. filifolia* “Pago Giant” plants from the bleach treatment that have now reached flowering stage have failed to produce pollen, while plants blooming from the GA3 treatment readily set pollen. *Byblis filifolia* “Hidden Valley” plants from the bleach treatment tend to be highly sensitive to leaf disturbance, with bumped or bent (even occasionally fed) leaves often wilting for no other apparent reason, but GA3 treated plants have shown no such response. *Byblis guehoi* from the bleach treatment appear to grow lankier, as scrambling vines rather than the bushy species they are typically known as, while GA3 seedlings are developing far more robustly and with denser growth (this may, however, be in part due to differences in the seed source material, and more testing will need to be done to determine if it is in fact the seed treatment or not that is resulting in this odd growth form). In *B. aquatica*, while the smallest plant is among those germinated from GA3, all plants from the GA3 treatment are flowering far more heavily than the singular plant that germinated from the bleach method. For the perennial species used, of course, no comparison can be made; bleach does not appear to be a viable option for germinating those species.

Figure 1 (left panel) shows representative photos that I was able to take of the germinating seedlings; Figure 1 (right panel) is of a selection of the flowering adult plants that have resulted.

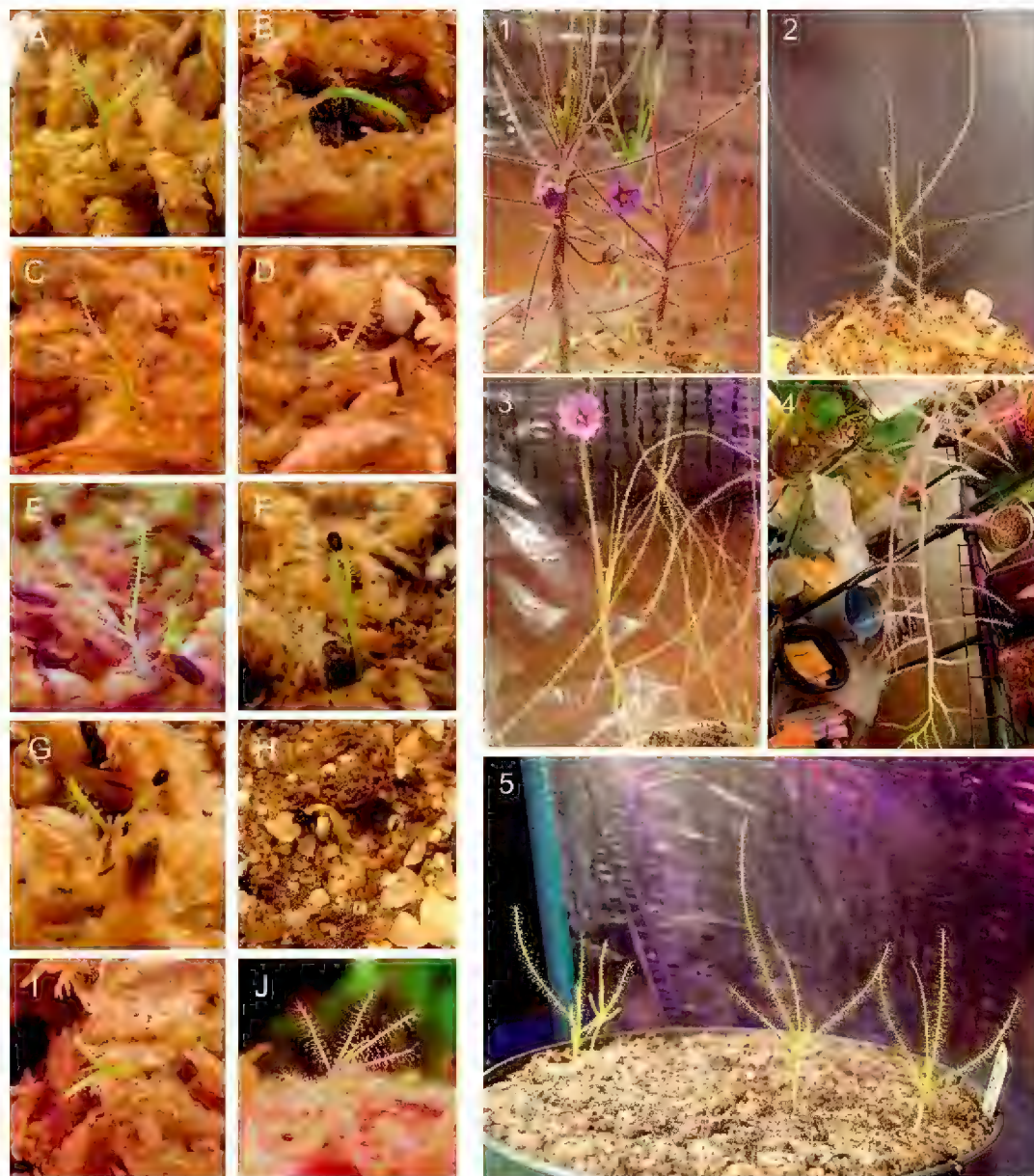


Figure 1: Left panel: A *B. aquatica* bleach treatment; B *B. aquatica* GA3 treatment; C *B. filifolia* “Hidden Valley” bleach; D *B. filifolia* “Hidden Valley” GA3; E *B. filifolia* “Pago Giant” bleach; F *B. filifolia* “Pago Giant” GA3; G *B. guehoi* GA3; H *B. lamellata* × *gigantea* GA3; I *B. rorida* “Lake Campion” GA3; J *B. rorida* “Lake Campion” bleach. Right panel: 1 *B. aquatica* “Robust Form” with GA3 plants in front and bleach plant in back; 2 *B. filifolia* “Hidden Valley” bleach plants; 3 *B. filifolia* “Pago Giant” bleach plant in bloom, but failing to produce pollen; 4 *B. guehoi* bleach plants demonstrating their lanky growth habit; 5 *B. lamellata* × *gigantea* GA3 seedlings.

From the preliminary results I’ve acquired from this, I am drawing the conclusion that despite ease of access, germination of *Byblis* seeds with bleach treatment is a far inferior method to GA3 (which is, luckily, becoming more readily available from more reliable sources). Further experimentation, particularly with the next generations of plants and hopefully other localities or species, is necessary for more definitive conclusions.

Among data already gathered as well but unable to be compared as only one treatment was used for each variety: *B. gigantea* germinates from 5-6 days of GA3 treatment similar to the *B. lamellata* × *gigantea* hybrid; *B. rorida* “Taylor’s Lagoon” successfully germinated from bleach treatment, but had poor overall germination rates; *B. liniflora*, while not technically needing any particular treatment, germinates at extremely high success and very rapidly after being give a 24-hour GA3 soak.

NEW CULTIVARS

Keywords: cultivar, *Nepenthes veitchii* ‘Jim Bockowski’, *Sarracenia leucophylla* ‘Mont Blanc’.

Nepenthes veitchii ‘Jim Bockowski’

Submitted: 1 March 2019

Nepenthes veitchii ‘Jim Bockowski’ (Fig. 1) is an impressively large and vigorous example of the prostrate form of *Nepenthes veitchii*. It produces a beautiful golden-striped peristome and was one of the first “highland” *N. veitchii* introduced into cultivation back in the 1980’s. The original plant was seed grown by Richard Sivertsen in the early 1980’s. Jim Bockowski received a cutting of this plant in the late 1980’s and it grew into one of the largest sized *N. veitchii* in cultivation. This is a female plant.

Jim Bockowski was an extraordinary horticulturalist and intrepid botanical explorer. He had a deep love for *Nepenthes* (as well as many other carnivorous genera) and was involved with the international carnivorous plant community for over 40 years. Jim passed away last year and this cultivar is being named in his memory.

Nepenthes veitchii ‘Jim Bockowski’ should be reproduced only by vegetative means to ensure that its unique characteristics are maintained.

—DREW MARTINEZ • Carnivero • Austin • Texas • USA • info@carnivero.com



Figure 1: *Nepenthes veitchii* ‘Jim Bockowski’ pitcher and plant after 3 m of vine was removed.

Sarracenia leucophylla ‘Mont Blanc’

Submitted: 21 February 2019

Sarracenia leucophylla ‘Mont Blanc’ (Fig. 2) is a plant from a batch of seeds from Walton County, Florida, collected by Georges Mac Kay. The seeds were sown in March 2003 by Thibault Barin, an excellent French collector of *Sarracenia*. He then selected some plants from the seedlings and one with the code name SL 30 culture was very vigorous. A few years later, a division of this plant came into the collection of Pierre Emmanuel Durand, great collector of *Sarracenia*, *Dionaea* forms, and *Drosera binata*. I have visited his collection many times, but only in the spring or summer and I never noticed this plant, which although very beautiful, did not stand out from other *S. leucophylla* growing next to it in his greenhouse. However, in November 2016, I had the opportunity to visit him for the first time in the fall and was impressed by the size of the fall pitchers.

I had never seen a *Sarracenia* so massive in proportions. Pitchers close to 1 meter high and almost 10 cm wide. I think it is possible to have even bigger pitchers on well-grown plants in big pots. The plant had been growing in a very large pots for so many years that it overflowed and the substrate was no longer very fresh. Pierre-Emmanuel was kind enough to offer me a piece. Once in its new substrate, the plant has grown vigorously and gratified me the following autumn with pitchers already having a good size.

Mont Blanc is the highest mountain in France, located in the Alps, in the department of Haute-Savoie, it is just on the border between France and Italy. It seemed appropriate to Thibault and me to give the name of this mountain, adorned with magnificent white glaciers, to this *Sarracenia*.

Sarracenia leucophylla ‘Mont Blanc’ should be reproduced only by vegetative means to ensure that the unique characteristics are maintained.

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—THIBAUT BARIN • La Pigne Le petit chalet • 26340 Aubenasson • France



Figure 2: *Sarracenia leucophylla* ‘Mont Blanc’.

NAMES OF CARNIVOROUS PLANT CULTIVARS REGISTERED IN 2018

Name	Publication	Date of registration
<i>Cephalotus</i> ‘Elizabeth’ C.Toole	Carniv.Pl.Newslett.47:126 (2018)	29 Sep 2018
<i>Dionaea</i> ‘Sensor’ S.Lascialfari	Carniv.Pl.Newslett.47:125 (2018)	29 Sep 2018
<i>Drosera</i> ‘Ghost’ K.Ivanez	Carniv.Pl.Newslett.47:75 (2018)	16 Jun 2018
<i>Drosera</i> ‘Hercules’ C.Trexler	Carniv.Pl.Newslett.47:38 (2018)	14 May 2018
<i>Nepenthes</i> ‘Black Widow’ R.Nunn & J.Chien	Carniv.Pl.Newslett.47:77 (2018)	16 Jun 2018
<i>Nepenthes</i> ‘Bronze Delight’ R.Nunn & J.Chien	Carniv.Pl.Newslett.47:82 (2018)	16 Jun 2018
<i>Nepenthes</i> ‘Caramel Candy Stripe’ R.Nunn & J.Chien	Carniv.Pl.Newslett.47:78 (2018)	16 Jun 2018
<i>Nepenthes</i> ‘Cherry Delight’ R.Nunn & J.Chien	Carniv.Pl.Newslett.47:81 (2018)	16 Jun 2018
<i>Nepenthes</i> ‘Chocolate Delight’ R.Nunn & J.Chien	Carniv.Pl.Newslett.47:80 (2018)	16 Jun 2018
<i>Nepenthes</i> ‘Lime Delight’ R.Nunn & J.Chien	Carniv.Pl.Newslett.47:79 (2018)	16 Jun 2018
<i>Pinguicula</i> ‘Riva’ M.Rubnitz	Carniv.Pl.Newslett.47:74 (2018)	16 Jun 2018
<i>Sarracenia</i> ‘Anne Carlisle’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:16 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Bella’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:19 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Birmingham Midnight’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:11 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Claire Soper’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:9 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Colin Clayton’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:18 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Dutch Stevens’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:13 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Ellie Wang’ M.Wang	Carniv.Pl.Newslett.47:127 (2018)	29 Sep 2018
<i>Sarracenia</i> ‘Flavona’ A.Amici	Carniv.Pl.Newslett.47:128 (2018)	29 Sep 2018
<i>Sarracenia</i> ‘Inspiration’ M.Srba & M.King	Carniv.Pl.Newslett.47:174 (2018)	28 Dec 2018
<i>Sarracenia</i> ‘Labyrinth’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:12 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Leviathan’ P.Young & S.Sullivan	Carniv.Pl.Newslett.47:37 (2018)	14 May 2018
<i>Sarracenia</i> ‘Lilianna’ P.Young & S.Sullivan	Carniv.Pl.Newslett.47:36 (2018)	14 May 2018
<i>Sarracenia</i> ‘Mary Cheek’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:21 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Max Rawlings’ C.Rawlings	Carniv.Pl.Newslett.47:172 (2018)	28 Dec 2018
<i>Sarracenia</i> ‘Mr Purplehaze’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:20 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Mr Sleepymonk’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:22 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Rita Soper’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:17 (2016)	29 Dec 2018
<i>Sarracenia</i> ‘Violet’ S.Drew & E.Erhart	RHS Trial Sarracenia for Sunny Windowsill:10 (2016)	29 Dec 2018



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